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Ecology of low-density forest tent caterpillar (*Malacosoma disstria*) populations:
pheromone monitoring methodology and the role of parasitoid alternative hosts.

by

B. Christian Schmidt



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

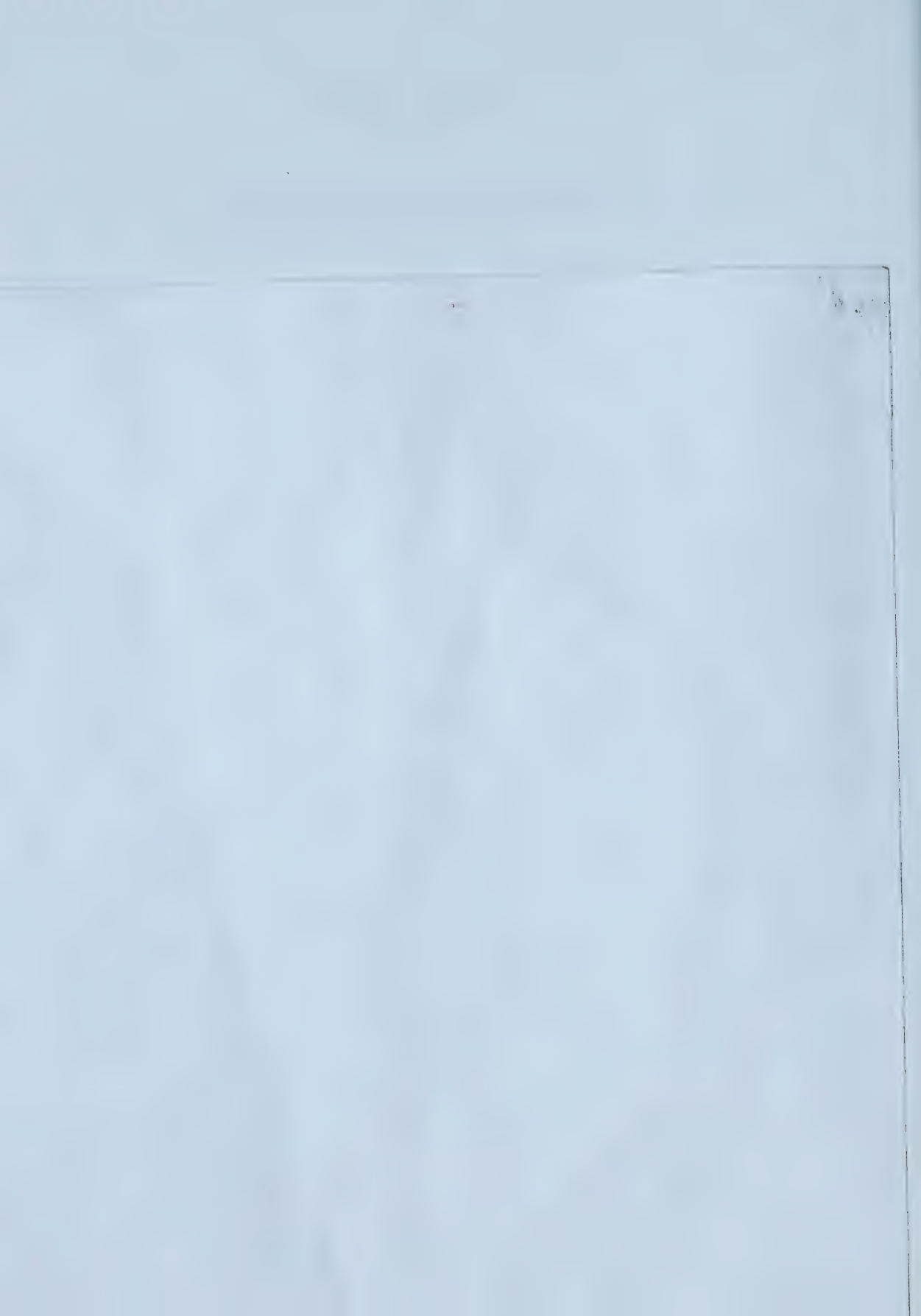
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Ecology of low-density forest tent caterpillar (*Malacosoma disstria*) populations: pheromone monitoring methodology and the role of parasitoid alternative hosts** submitted by B. Christian Schmidt in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.



dedicated to my parents

Abstract

To effectively monitor forest tent caterpillar (FTC) (*Malacosoma disstria* [Hbn.]) populations, a trapping system using synthetic sex pheromones was evaluated. Three pheromone blends were field-tested, consisting of 1) [5Z,7E] 5,7 dodecadienal, 2) 100:1 [5Z,7E] 5,7 dodecadienal : [5Z,7Z] 5,7 dodecadienal and 3) 100:1:10 [5Z,7E] 5,7 dodecadienal : [5Z,7Z] 5,7 dodecadienal : Z,7 dodecanal. Relative to the other blends, trap catches using the tertiary blend (3) suggest that this pheromone is superior for capturing FTC moths. Lures dosed with 11 µg or less of either the binary (2) or tertiary blends failed to capture moths in endemic FTC populations, while lures dosed at 390 µg gave the highest mean trap catch and the lowest rate of zero-captures. Trap efficacy is improved by the use of polyurethane lures (Flex Lure, Phero Tech Inc., Delta, B.C.) compared to red rubber septa lures, because attractiveness of Flex Lures remains constant over at least the first 28d in the field. The Universal Moth Trap is superior to the Sticky Wing Trap for capturing moths, at both endemic and epidemic population levels.

The potential role of parasitoid alternative hosts in FTC population dynamics was explored through investigating the effects of anthropogenic forest fragmentation on host assemblages. Most arboreal lepidopteran hosts (68%) either declined in abundance or were less likely to occur at sites with lower surrounding forest cover. Arboreal (vs. grass- and herb-feeding) Lepidoptera are the most important alternative hosts of FTC parasitoids. Diversity of the host assemblage showed a marked decline with increasing forest fragmentation. The implications of forest structure-mediated changes in the parasitoid host assemblage are discussed in light of FTC population dynamics.

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Chapter 1

GENERAL INTRODUCTION

BACKGROUND

The population ecology of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), has received considerable attention from a wide variety of disciplines, including theoretical population ecology, landscape ecology, insect-plant and predator-prey biology, behavioural ecology and forestry (see Otvos *et al.* [1998] for an overview). Members of the genus *Malacosoma* are among the most extensively studied lepidopterans (Fitzgerald 1995), in large part because of their periodic abundance and dramatic eruptive population dynamics. The best example of a species exhibiting widespread, naturally occurring outbreaks is probably the forest tent caterpillar (FTC), which has historically had the largest outbreak area of any insect in the United States (Batzer *et al.* 1995). Densities of mature FTCs during an outbreak can be reasonably estimated at approximately 750,000 larvae per hectare of mature aspen forest (Batzer *et al.* 1995), which corresponds to more than 1000 kg of FTC biomass per hectare. Very few, if any, animal species reach these proportions in a terrestrial ecosystem.

Given the attention the forest tent caterpillar has received in the scientific community, it is somewhat surprising that very little empirical data are available on tent caterpillar ecology during the endemic population phase (but see Parry *et al.* [1997]). One of the main impediments to studying endemic FTC populations has been the logistic difficulty of accurately determining FTC abundance. When abundance levels fall below the detection threshold of traditional estimating methods, such as egg mass counts (Shepherd & Brown 1971), FTC population size cannot be determined. As in monitoring programs for other economically important Lepidoptera, trapping of FTC moths using synthetic sex

pheromones provides a solution to this. Pheromone-trap monitoring has the potential to precisely and accurately measure population densities over a range of abundances, which can vary over several orders of magnitude. Predicting FTC outbreaks and monitoring their greatly fluctuating populations for managing aspen harvest regimes has also become desirable, since outbreaks often result in the growth reduction and die-back of the FTC's primary larval host, trembling aspen (*Populus tremuloides* Michx.) (Churchill *et al.* 1964, Pendrel 1991). The increased value of trembling aspen as a timber product, and the resulting change in economic attitudes, has been paralleled by increased interest in insects and diseases affecting aspen (Bryson 1989).

FTC mating biology

The forest tent caterpillar is univoltine throughout its range (Stehr & Cook 1968), and eclosion of adults peaks between mid- and late July in central Alberta (Chapter 3). Females are sexually mature upon emerging, which occurs late in the afternoon or early evening (Bieman & Witter 1983). Male moths become active earlier in the day, and can initiate mate searching as early as mid-afternoon (Shepherd 1979). Mate location in *Malacosoma* is mediated by a sex pheromone emitted by the female; evidence suggests that male *Malacosoma* do not produce courtship pheromones (Coroiu *et al.* 1986). Mate attraction by pheromone has two obvious advantages: males can locate females at very low population densities, and mating success is increased over the relatively short adult lifespan.

The sex pheromone of female FTC is emitted from a gland between the 8th and 9th abdominal segments, visible as a smooth saddle-shaped area during calling behaviour (Percy & Weatherston 1971). Pheromone synthesis occurs during the pupal stage in *Malacosoma neustria* (Coroiu *et al.* 1986), and presumably also in FTC. Although it was once believed that lepidopteran pheromones were derived from secondary host plant compounds (Hendry *et al.* 1975), it is now known that pheromone is synthesized *de novo*. Roelofs & Wolf (1988) suggest that most moth species produce pheromone components from palmitic acid, which is derived from acetate via the fatty acid cycle within the gland tissue. The physiological response of male FTC to pheromones is mediated by neural receptors on the antennae, where pheromone molecules bind to receptor proteins on the neuron membrane and subsequently elicit neural impulses (Hansson 1995).

Sex pheromones in Lepidoptera consist of precise compound blends, and the variation in compound proportions within a population of any species is generally very low. Bjostad *et al.* (1987) summarized the elements of lepidopteran pheromones into three variables: 1) Chain length, usually straight-chained molecules with even numbers of carbon atoms (10, 12, 14, 16 or 18), 2) functional group (alcohol, acetate, or aldehyde), and 3) double bonds (unsaturation), varying in number from one to three with a *Z* or *E* configuration. The presence of a sex pheromone in the FTC was first reported by Struble (1970), although the specific pheromone components were unknown at the time. Ten years later, Chisholm *et al.* (1980) found that a straight-chained 12-carbon aldehyde, Z5,E7 dodecadial, and the corresponding alcohol, were two principal components. Although all four isomers of the C₁₂ - 5,7 aldehydes, alcohols and acetates were evaluated using

electro-anntenogram and behavioural bioassays, only the Z,E aldehyde and alcohol were field tested (presumably because these elicited the greatest response). Furthermore, Chisholm *et al.* (1980) showed that male antennal stimulation occurred in response to a range of mono-unsaturated C₁₂ aldehydes, although these compounds did not attract males in the field. The Z,Z aldehyde isomer and mono-unsaturated Z7 dodecanal were subsequently reported to increase the attractiveness of 5Z,7E aldehyde in the field (unpublished results cited in Chisholm *et al.* 1982), although it was previously shown that these Z,Z and Z aldehydes were not effective field lures when used alone (Chisholm *et al.* 1980). The molecular structures of the active compounds known to occur in FTC sex pheromone are shown in Figure 1.1.

FTC population dynamics

There are a number of factors that may operate within endemic insect populations that could initiate outbreaks, both intrinsic (e.g. genetic or physiological properties of individuals, life history strategies) and extrinsic (e.g. environmental and climatic changes, predator-prey interactions). Although collapse of FTC outbreaks is primarily attributed to predators, pathogens and parasitoids (Witter & Kulman 1972, Parry 1995, Roland & Taylor 1997), the cause of outbreaks remains for the most part speculative. Berryman (1987) gives a summary of hypotheses for the initiation of insect outbreaks. Specialist parasitoids and pathogens play a vital role in epidemic and collapsing FTC populations, whereas generalist parasitoids and avian predators appear to be important mortality sources in endemic populations (Parry *et al.* 1997, J. Roland, unpublished data). Favorable winter and spring weather conditions facilitate outbreak initiation (Cooke *in*

prep), and may allow FTC to increase to levels where they can escape regulation by predators and parasitoids.

Forest fragmentation and FTC - parasitoid dynamics

The effects of landscape structure on aspects of invertebrate ecology, ranging from community structure to ecosystem function, have been of central concern to insect ecologists, primarily as a result of increased conservation efforts due to habitat destruction (Tscharnkte 2000). Since parasitoids figure prominently in most insect predator-prey systems (Hochberg & Ives 2000), numerous studies have also begun to address the effects of landscape structure on parasitoid ecology (see Roland [2000] for a review). A large body of literature has accumulated concerning the effects of landscape structure (defined over a wide range of spatial scales) on patterns of species abundance and diversity, initiated with the pioneering work on island biogeography and species-area relationships (MacArthur & Wilson 1967, Simberloff & Wilson 1970). However, abundance and diversity patterns are as varied as the context in which the term 'landscape structure' is used; for example, Daily & Ehrlich (1995) showed that butterfly assemblages are less species-rich in small forest fragments, whereas others have shown that species richness increases in smaller fragments due to the invasion of species from outside of the fragments (e.g. Brown & Hutchings 1997). Very few studies have attempted to link patterns induced by forest fragmentation to functional processes. Didham *et al.* (1996) summarize the need for these kinds of studies and suggest research guidelines.

The forest tent caterpillar is one of relatively few species that has provided ecologists with a model parasitoid - prey system with which to gain insight into landscape structure effects on population processes. Forest tent caterpillar outbreak characteristics are modified by forest structure (Roland 1993), and forest heterogeneity likely also affects processes governing population eruption (Cooke *in prep.*, Chapter 4). It is well established that parasitoid-caused mortality exhibits a variety of patterns according to the spatial structure of prey individuals (Latto & Hassell 1988), including parasitoids of the FTC (Roland 2000). Parasitoids that specialize on FTC are coupled to the population changes of FTC, and may therefore be subject to local extinctions as a result of spatial variation in FTC abundance. In contrast, generalist parasitoids, which are able to prey on hosts other than FTC, are at an advantage since they are not coupled to extremely low FTC densities. As pointed out by Latto & Hassell (1988), the consequences of spatial density dependence (or lack thereof) in generalist predators (vs. specialist predators) to the interacting populations have been neglected. The influence forest structure has on FTC - parasitoid interactions may be exacerbated by spatial changes in the host community of generalist parasitoids. Landscape structure effects on parasitism mediated by host abundance and diversity have been noted in other host-parasitoid systems within agricultural landscapes (Tscharntke 2000, Kruess & Tscharntke 2000).

THESIS OVERVIEW

To attempt a more complete understanding of the population biology of the FTC, a more thorough knowledge of FTC ecology during the endemic population stage is necessary. The objectives of this thesis are to provide improved population monitoring and

estimation techniques. Furthermore, I address one aspect of low-density FTC population dynamics, by examining the effects of forest structure on the host community of parasitoids.

The development of an effective pheromone monitoring protocol for forest tent caterpillar hinges on a variety factors, both direct (pheromone chemistry) and indirect (lure and trap effects on catch efficacy). Fundamentally important are pheromone formulation and release rate. Many sex pheromones only function as attractants when several chemical components are present, combined in optimum ratios (Roelofs & Carde 1977). If the volatility of the components differs, the lure may change in attractiveness over time and consequently give inconsistent results. Lure dosage is crucial to trap performance, because the pheromone release rate must be within a restricted range in order to produce maximum trap catches (Roelofs & Carde 1977).

In Chapter 2, I address the effects of pheromone chemistry through field trials on pheromone blend and dosage. The pheromone components tested in the blend trials consist of three of the four known active compounds ([5,7] 5Z,7E dodecadienal, [5,7] 5Z,7Z dodecadienal, and Z7 dodecanal), with ratios and concentrations based on the results of Chisholm *et al.* (1980) and Palaniswamy *et al.* (1983). Where possible, field trials were carried out in both endemic and epidemic FTC populations to evaluate trapping efficacy over the range of FTC population variability.

In order to provide accurate population estimates of FTC, it is also necessary to consider the field protocol of trap deployment, in conjunction with an optimum lure-trap system. Traps should be able to capture moths over the range of variation in population abundance, exhibit consistent efficiency from year to year and have low catch variability (all else being equal). In Chapter 3, I compare the performance of the rubber septum traditionally used as a pheromone dispenser in insect monitoring programs, to a polyurethane lure developed by Phero Tech Inc. (Delta, BC). Two trap designs are also compared: a sticky-type trap (Wing trap) often used for monitoring lepidopteran pests, and a high capacity bucket-type trap (Universal Moth Trap). Finally, I address the timing of trap deployment and lure longevity in the field in relation to the flight period of FTC moths.

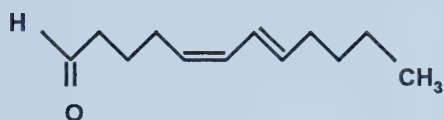
In Chapter 4, I assess whether changes in forest cover have positive or negative effects on FTC parasitoid hosts, and how these changes in host community structure might help explain spatial and temporal patterns in FTC population cycles. By quantifying the amount of forest cover over a range of spatial scales, I evaluate the effects of anthropogenic habitat fragmentation (primarily agriculture) on the abundance and diversity of Lepidoptera in the boreal forest of central Alberta. Specifically, the potential consequences of spatially patterned changes in the assemblage of lepidopterans that are hosts to FTC parasitoids are discussed in light of published parasitoid host ranges.

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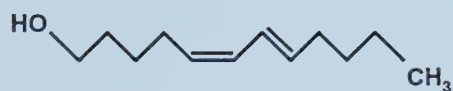
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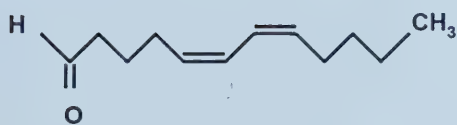
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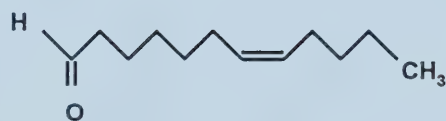
Z5,E7 dodecadienal



Z5,E7 dodecadien-1-ol



Z5,Z7 dodecadienal



Z7 dodecanal

Figure 1.1: Molecular structure of active compounds in the female sex pheromone of *M. disstria*.

Chapter 2

OPTIMIZATION OF SYNTHETIC PHEROMONES FOR MONITORING FOREST TENT CATERPILLAR POPULATIONS

INTRODUCTION

The use of semiochemicals has been an integral part of insect pest management for several decades. Pheromone trapping has proven to be a superior population-monitoring tool because pheromone traps are simple to maintain and operate, target only one species, and lures and traps are effective even at very low population densities. Pheromone traps also provide the potential for monitoring a large geographical area with relatively little effort. Many economically important Lepidoptera are monitored using sex pheromones, including the gypsy moth (*Lymantria dispar* [L.]), Douglas-fir tussock moth (*Orgyia pseudotsugata* [McD.]), western spruce budworm (*Choristoneura occidentalis* [Free.]) and spruce budworm (*C. fumiferana* [Clem.]) (Grant 1991).

Although the forest tent caterpillar, *Malacosoma disstria* Hübner, (subsequently referred to as FTC) is a widespread defoliator of deciduous trees in North America, its cyclic outbreaks have been relatively economically unimportant because its principal host, trembling aspen (*Populus tremuloides* Mchx.), has traditionally been non-marketable. As a result, no optimized pheromone trapping protocol currently exists for FTC. Recent changes in forest management practices have, however, shifted the perspective on the status of FTC as a pest; The increasing economic value of trembling aspen has made FTC monitoring an important potential predictive tool of FTC outbreaks, since defoliation causes substantial growth losses and increase disease susceptibility (Churchill *et al.* 1964, Pendrel 1991).

The forest tent caterpillar affords ecologists with an excellent model insect with which to gain insight into population dynamics. Virtually all studies of FTC dynamics, however, have been carried out in epidemic populations (e.g. Tomlinson 1938, Sippell 1957, Witter *et al.* 1975, Witter & Kulman 1979, Witter 1979, Varley *et al.* 1974, Harmsen & Rose 1984, Smith & Goyer 1986, Bowers *et al.* 1993, Roland 1993, Myers & Kukan 1995, Roland & Taylor 1997). This is in part due to the lack of monitoring techniques effective over a wide range of FTC densities. The importance of an optimum pheromone trapping protocol is therefore two-fold: to provide a predictive monitoring tool for forest

management practices, and to provide a precise measure of endemic population density for studies on population dynamics.

The effectiveness of synthetic sex pheromone lures for insect population monitoring is fundamentally dependent on the pheromone formulation and release rate. Many sex pheromones only function as attractants when more than one chemical component is present, and the ratios of these components are critical. If the volatility of the components differs, the lure may change in attractiveness over time and consequently give inconsistent results. The pheromone release rate must generally be within a restricted range in order to produce maximum trap catches (Roelofs & Carde 1977), so lure dosage is crucial to trap performance. The objective of this study was to determine the optimum pheromone lure formulation and dosage for monitoring populations of the forest tent caterpillar. I evaluated the field performance of traps baited with several lure blends and concentrations of 12-carbon alcohols and aldehydes based on the work of Chisholm *et al.* (1980) and Palaniswamy *et al.* (1983), which characterized the main FTC pheromone components.

METHODS AND MATERIALS

Study sites

All field-testing of synthetic pheromones and traps was done at two FTC population densities: an epidemic (outbreak) and endemic (non-outbreak) population. Aspen stands 20 km SW of Prince George, British Columbia, were chosen as sites with an epidemic FTC population; this area has exhibited visible defoliation prior to and during the study (1995 - 2000 [S. Lindgren, pers. comm.]). The Prince George site is characterized by mixed wood forest within the sub-boreal spruce biogeographic region (Meidinger & Pojar 1991). Forest at this site is dominated by trembling aspen, interspersed with white spruce (*Picea glauca*), paper birch (*Betula papyrifera*) and Balsam poplar (*Populus balsamifera*). Understory shrubs were predominantly red osier dogwood (*Cornus stolonifera*), wild rose (*Rosa* spp.), and saskatoon (*Amelanchier alnifolia*).

The second study site was located in the southeast corner of the Cooking Lake - Blackfoot Recreation Area (112° 47' W, 53° 28' N) in the Ministik Hills of central Alberta. There has not been any detectable defoliation at this site since the collapse of an FTC outbreak in 1996 (J. Roland, unpublished data), and was hence chosen for field trials representative of endemic FTC densities. The Ministik Hills are within the dry boreal mixed wood ecoregion of Alberta (Strong & Leggat 1992), and the natural vegetation is dominated by trembling aspen forest. Balsam poplar occurs as a dominant or co-dominant species in more mesic sites. Paper birch, white spruce, and black spruce (*Picea mariana*) occasionally form small, isolated stands. In upland sites, beaked hazel (*Corylus cornuta*) often forms a thick understory. Other common understory shrubs include red raspberry (*Rubus idaea*), red osier dogwood, Bebb's willow (*Salix bebbiana*) wild rose (*Rosa* spp.), saskatoon, and pin cherry (*Prunus pennsylvanica*).

Pheromone Blend

An overview of the three pheromone blends tested during this study is presented in Table 2.1. Based on results obtained by Palaniswamy *et al.* (1983), performance of (5Z,7E) 5,7 dodecadial (subsequently referred to as ZE) and a blend of 100:1 (5Z,7E) 5,7 dodecadial : (5Z,7Z) 5,7 dodecadial (subsequently referred to as ZE:ZZ) were compared. Corresponding alcohols of these aldehyde isomers were synthesized using Wittig condensation reactions (followed by oxidation to aldehydes) by Phero Tech Inc., Delta, BC (Chisholm *et al.* 1980, and references therein). These aldehydes were loaded onto a polyurethane tube pheromone dispenser (Flex Lure, Phero Tech Inc.) at 67 µg per lure, and deployed in the field inside Sticky Wing Traps. All lures and traps used in this study were obtained from Phero Tech Inc.

Traps were set out following a randomized block design, each block consisting of the two pheromone blend treatments in addition to a 'pheromone dispenser' treatment (see Chapter 3). Individual traps were placed approximately 100 m apart along transects through mature aspen stands, and were hung between 1.5m and 2.0m above ground level. Traps were set out in mid-July of 1998, about two weeks prior to the emergence of FTC adults. Blocks at the Prince George site were assigned according to levels of visible

defoliation caused by FTC in 1998. Among all sites, four FTC population density categories were assigned to each block, ranked according to defoliation levels: no defoliation (Ministik Hills), low to moderate, moderate to high, and high to severe defoliation (Prince George). Traps were collected in late August to early September, and trap contents were sorted and the numbers of male FTC moths were tallied. Because 5,7 dodecadienal isomers are also pheromone constituents of the western tent caterpillar (Chisholm *et al.* 1981), *Malacosoma californicum* Packard, moths were screened for the presence of this species. All captured *Malacosoma* proved to be *M. disstria*.

In 1999, I compared the binary blend (ZE:ZZ) tested in 1998 to a tertiary blend, consisting of ZE:ZZ with the addition of Z,7 dodecanal (this blend is subsequently referred to as ZE:ZZ:Z). The concentrations used were 90µg (100:1 ZE:ZZ) and 95µg (100:1:10 ZE:ZZ:Z) per Flex Lure. Trapping protocol was identical to that used in 1998, but the Universal Moth Trap, or Unitrap, was used in place of the Wing Trap. Unitraps were chosen for their higher catch capacity because at high density, Wing Traps quickly become saturated with moths (see Chapter 3). Each sample block consisted of six treatments: one ZE:ZZ:Z treatment, and five “pheromone dose” treatments (see below). These treatments are summarized in Table 2.1 and 2.2. Defoliation levels by FTC at the Prince George sites were not categorized in 1999, since most sites exhibited heavy defoliation. FTC density categories were therefore ranked according to the mean number of moths for each block. This precluded statistical comparison among the epidemic sites, but allowed for meaningful data presentation with which to evaluate lure performance as a function of overall FTC density.

Statistical Analyses

To compare the performance of the primary (ZE) to secondary (ZE:ZZ) blends over a range of FTC population levels, I conducted an analysis of variance on trap catch among the sites assigned one of the four defoliation categories. Methods for non-parametric multiple comparisons with unequal sample sizes were used (Zar 1999), using the SYSTAT 9.0 statistical software package (SPSS 1999).

I also compared the overall performance of primary to secondary blends at endemic and epidemic FTC levels; in order to do this, the epidemic (Prince George) sites were pooled and compared to endemic sites, using non-parametric methods for a two-sample t test (Zar 1999). The 1999 data comparing trap catch of secondary to tertiary blends were analyzed in a similar manner, with the exception of the fact that epidemic sites did not have to be pooled.

Pheromone Dose

Catchability of FTC moths with varying dosages of secondary and tertiary blends was field-tested in 1999 and 2000, respectively (Table 2.2). The Flex Lure was used as a dispenser in all cases, with concentrations of 1 μg , 8 μg , 67 μg , 90 μg , 390 μg (ZE:ZZ) and 1 μg , 11 μg , 110 μg (ZE:ZZ:Z). Lures were deployed within Unitraps, in a similar randomized block design discussed under "Pheromone Blend". ZE:ZZ was tested at both the Prince George and Ministik sites, while ZE:ZZ:Z was tested only at the Ministik site.

Statistical Analyses

To determine if lure dose had a significant effect on trap catch, I conducted non-parametric analyses of variance, followed by multiple comparisons (Zar 1999) among lure dosages. Trap catch of Lepidoptera using pheromones is not a linear function of pheromone concentration, but is generally characterized by diminishing returns in captures with increasing amounts of pheromone, with a maximum concentration beyond which trap catch decreases (Roelofs 1978). I performed a polynomial regression to examine the functional response of moths captured with increasing pheromone (ZE:ZZ) dose (MathSoft 1999). To minimize the variation in trap catch attributable to spatial variation in FTC population density, I first standardized values of trap catch according to sample blocks. This was achieved by converting moth counts to Z-scores (Zar 1999), based on the mean and standard deviation of the sample block from which the trap catch originated. A quasi-likelihood function was used to estimate the model because Poisson regression assumptions were not met due to overdispersion. Quasi-likelihood estimates are not affected by under- or over-dispersion (McCullagh & Nelder 1989). Pheromone

dose trials using the tertiary blend yielded trap catches only at the 110 µg dosage, so these trials were not amenable to further analysis.

RESULTS

Pheromone Blend

Overall, the tertiary pheromone blend consistently caught more moths than did either the secondary or primary blends (Fig. 2.1). Although the primary and tertiary blends were not tested in the same year, both these blends were compared to ZE:ZZ. To allow comparison among all blends, ZE:ZZ therefore served as a 'control blend'. Trap catch is therefore shown relative to the ZE:ZZ catch in Fig. 2.1. The mean number of FTC caught using the tertiary blend was about three times higher than that of the ZE:ZZ trap catch (Fig 2.1). The total ZE and ZE:ZZ trap catches were very similar; however, these results are misleading because these blends were compared using Wing Traps. The sticky surfaces of the Wing Traps become saturated with moths when FTCs are abundant, and trap efficiency decreases with moths captured. Wing Trap catch at high FTC densities is therefore similar among pheromone treatments. The difference in trap catch between ZE and ZE:ZZ in Wing Traps becomes evident at low FTC density. Although ZE and ZE:ZZ appear to have similar discriminatory ability among defoliation categories (Fig. 2.2), ZE:ZZ had significantly higher trap catch than ZE at the endemic sites (Fig. 2.3a). The low trap catch of ZE at endemic levels results in a truncated frequency distribution, and the median is 'veiled' unlike that of ZE:ZZ (Fig. 2.3a).

Compared to ZE:ZZ, the tertiary blend provided greater catch precision: Figure 2.4 shows that at low "density" ranks, the interquartile range in trap catch using ZE:ZZ:Z is smaller, with a discernible median value for all ranks (median values for ranks three and five lie on top of box limits and are therefore not visible). Conversely, the median values using ZE:ZZ at density categories one, two, and three are not evident due to the large number of zero-catches. Although the ZE:ZZ trap catch at the epidemic FTC sites (Prince George) is less variable than that of ZE:ZZ:Z (Fig. 2.5b), the ability of ZE:ZZ to resolve FTC levels at the endemic site is poor due to a high number of zero-catches (Fig.2.5a). At

higher trap catches, all blends have comparable interquartile ranges (Fig. 2.2 and 2.4), and should therefore give equally precise estimates of FTC populations.

Dose

Trap catch generally increased with increasing ZE:ZZ pheromone dose per lure. With the exception of one sample, the 1 µg and 8 µg lures failed to catch any moths in the endemic FTC populations (Fig. 2.6). The 67 µg and 90 µg lure doses yielded somewhat anomalous results, since the 67 µg lure consistently captured more moths than did the 90 µg lure (Figs. 2.6, 2.9). The 390 µg lure dosage resulted in the highest mean trap catches in both endemic and epidemic populations (Fig. 2.6). In terms of ability to detect FTC levels, the 390 µg lure had the most frequent successful trap catches at low densities, (Fig. 2.9), while the 1 µg and 8 µg lures had predominantly failed catches at all but the highest density categories (Fig. 2.9).

Polynomial regressions of trap catch on lure dose revealed that a second order polynomial best explained variation in trap catch ($p < 0.05$, $r^2 = 0.48$). Trap catch per unit of pheromone decreased with increasing dosage, and there was some evidence that the optimum lure dose for ZE:ZZ may be between 90µg and 390µg; however, the fact that doses between 90µg and 390µg were not tested prevented the resolution of the response curve between these doses with any certainty.

DISCUSSION

To provide the best estimate of FTC population levels, trap catch of adult FTC using synthetic pheromones should be precise, and operate over as wide a range of FTC densities as possible. The lower limit of the pheromone performance range is set by the lowest FTC density at which the pheromone is able to trap moths, while the upper limit is determined by trap capacity. Therefore, a pheromone that is able to attract moths at the lowest population levels, without saturating trap catch in epidemic populations, should be the optimum lure. Although all of the pheromone blends tested exhibited comparable variation in trap catch (and should therefore give equally precise population estimates), the three-component blend (100:1:10 [5Z,7E] 5,7-dodecadienal : [5Z,7Z] 5,7-

dodecadienal : [Z] 7-dodecanal) was best able to detect FTC adults at the lowest population levels. Z,E dodecadienal is the principal component of the FTC sex pheromone (Chisholm *et al.* 1980), and small proportions of Z,Z dodecadienal and 7,Z dodecanal appear to act as potentiators of Z,E dodecadienal. 7,Z dodecanal elicits electro-antennogram responses in male *M. disstria*, but it does not attract males in the field when tested alone or in combination with other mono-unsaturated dodecanals (Chisholm *et al.* 1980). Chisholm *et al.* (1982) showed that *M. disstria* orientation to traps could be effectively disrupted using secondary pheromone blends similar to the one tested. Furthermore, they showed that traps baited with three live virgin female *M. disstria* caught as many moths as did those baited with 120µg lures of 10:1:1 ZE:ZZ:Z.

The addition of the Z,Z isomer to Z,E dodecadienal marginally improved lure performance at low FTC levels. At high FTC trap catches, ZE and ZE:ZZ were equally effective. This may be the result of the trap design used in this experiment; Wing Traps use a sticky surface to capture moths entering the trap, but the sticky surface becomes increasingly covered with scales and hairs as more moths enter. The success rate of the trap therefore decreases with each additional moth, and the difference in the lure performance may have been masked by the inability of the trap to retain additional moths. Similarly, Chisholm *et al.* (1982) found no difference in the ability of ZE:ZZ (64µg : 6.4µg) to disrupt male orientation compared to ZE-only lures.

At high ambient pheromone concentrations, FTC response to pheromone traps is disrupted (Palaniswamy *et al.* 1983), presumably because physiological response reaches a saturation point and males cannot orient to the pheromone source. A maximum lure dosage can therefore be expected, above which the moth's ability to orientate to the trap decreases. Whether the optimum ZE:ZZ dose occurs between 90µg and 390µg, or above 390µg, remains unclear. Additional concentrations should be tested to resolve where the optimum occurs (Fig. 2.7). It is evident however, that the trap catch is not a linear function of lure dose over the range tested. There is a diminishing return in trap catch per unit of pheromone up to at least 390µg. Lure concentrations of 1µg and 8µg were too low to capture moths in the endemic FTC population.

Although the tertiary pheromone (ZE:ZZ:Z) is more effective overall, it seems to elicit male FTC response over the same dose range as the binary blend (ZE:ZZ).

Concentrations of 1µg and 11µg failed to capture moths at endemic FTC sites, whereas 110µg lures averaged 2.5 moths / trap (Fig. 2.8). The optimum lure dose for ZE:ZZ:Z is not known, but Chisholm *et al.* (1982) report orientation disruption of FTC males by ZE:ZZ:Z at a release rate of 241µg / 24h in an 81m² plot.

The highest trap catch of *M. disstria* were consistently obtained with the three-component aldehyde lure, comprised of the Z,E and Z,Z isomers of 5,7 dodecadial and the corresponding monounsaturated aldehyde 7,Z dodecanal. At a ratio of 100:1:10 (ZE:ZZ:Z), Flex Lures dosed with 95µg and 110µg attracted moths in both epidemic and endemic *M. disstria* population levels, but 1µg and 11µg lures failed to do so. A pheromone trapping protocol for the forest tent caterpillar should be standardized using a blend of 100:1:10 ([5Z,7E] 5,7-dodecadial : [5Z,7Z] 5,7-dodecadial : [Z] 7-dodecanal), at a dosage of approximately 100µg. This should provide a superior lure for monitoring FTC populations at all densities. Further field trials should be conducted to determine at what concentrations lures saturate male response.

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Table 2.1: Synthetic *M. disstria* pheromone blends tested in this study.

Code	Ratio	Constituents	Year Tested
ZE	----	(5Z,7E) 5,7 dodecadienal	1998
ZE : ZZ	100:1	(5Z,7E) 5,7 dodecadienal : (5Z,7Z) 5,7 dodecadienal	1998, 1999
ZE : ZZ : Z	100:1:10	(5Z,7E) 5,7 dodecadienal : (5Z,7Z) 5,7 dodecadienal : Z7 dodecanal	1999

Table 2.2: Concentrations of *M. disstria* pheromone blends tested in this study. Abbreviations are those given in Table 2.1.

Code	Ratio	Load	Year Tested
ZE	----	67 µg	1998
ZE : ZZ	100:1	1 µg, 8 µg, 67 µg, 90 µg, 390 µg	1999
ZE : ZZ : Z	100:1:10	1 µg, 11 µg, 110 µg	2000

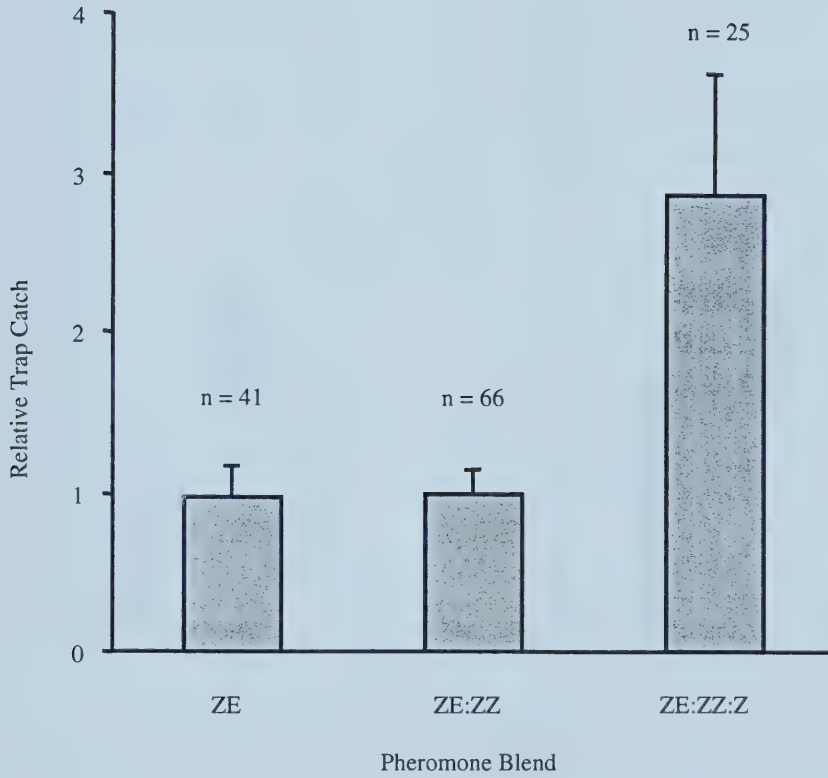


Figure 2.1: Relative *M. disstria* trap catch (as proportion of ZE:ZZ) among pheromone blends (+ standard error). Abbreviations as those given in Table 2.1.

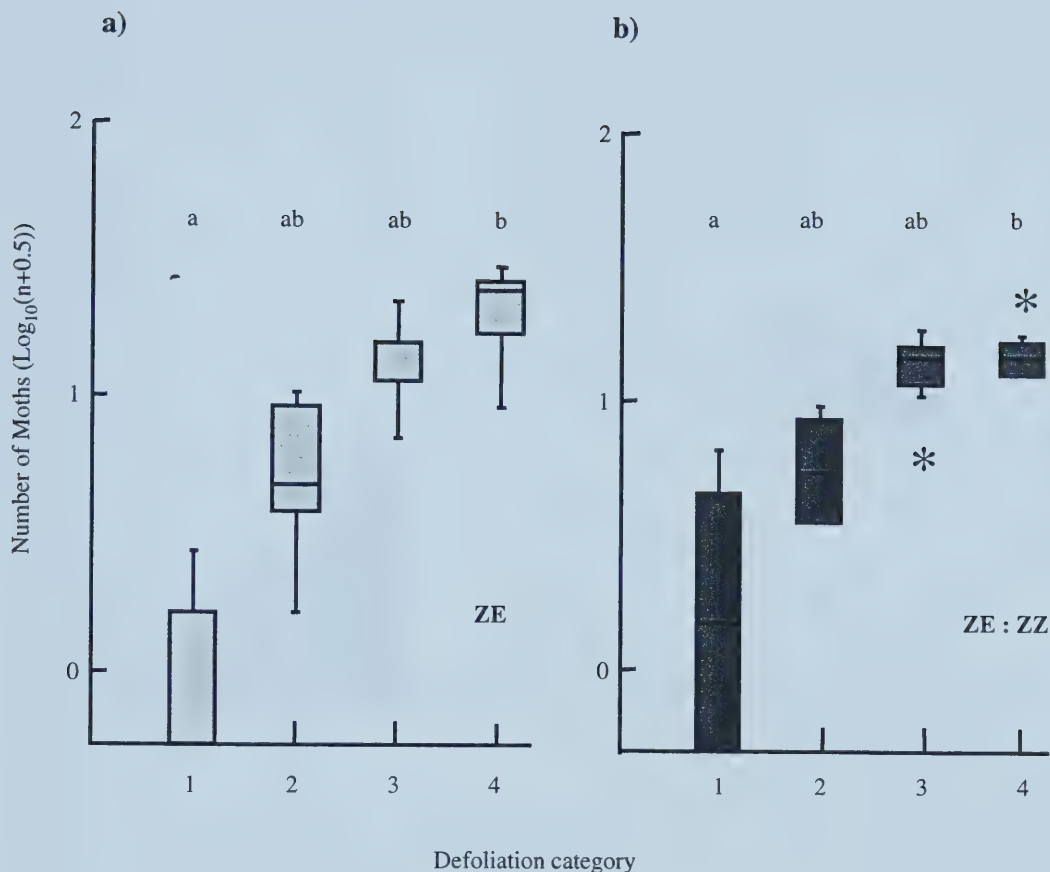


Figure 2.2: Number of *M. disstria* caught (box and whisker plots) using **a)** the ZE-only and **b)** ZE:ZZ pheromone blends. Pheromone abbreviations are defined in Table 2.1. Aspen defoliation categories are 1) None ($n = 21$), 2) light - moderate ($n = 6$), 3) moderate - heavy ($n = 7$), 4) heavy - severe ($n = 7$). Moth counts with the same letter above them are not significantly different from each other ($\alpha = 0.05$). The interquartile range is bounded by the box, with the horizontal dash indicating the median. Whiskers represent data points within 1.5 interquartile ranges of the upper and lower quartiles. Outliers are indicated by asterisks and circles (within and beyond three interquartile ranges, respectively).

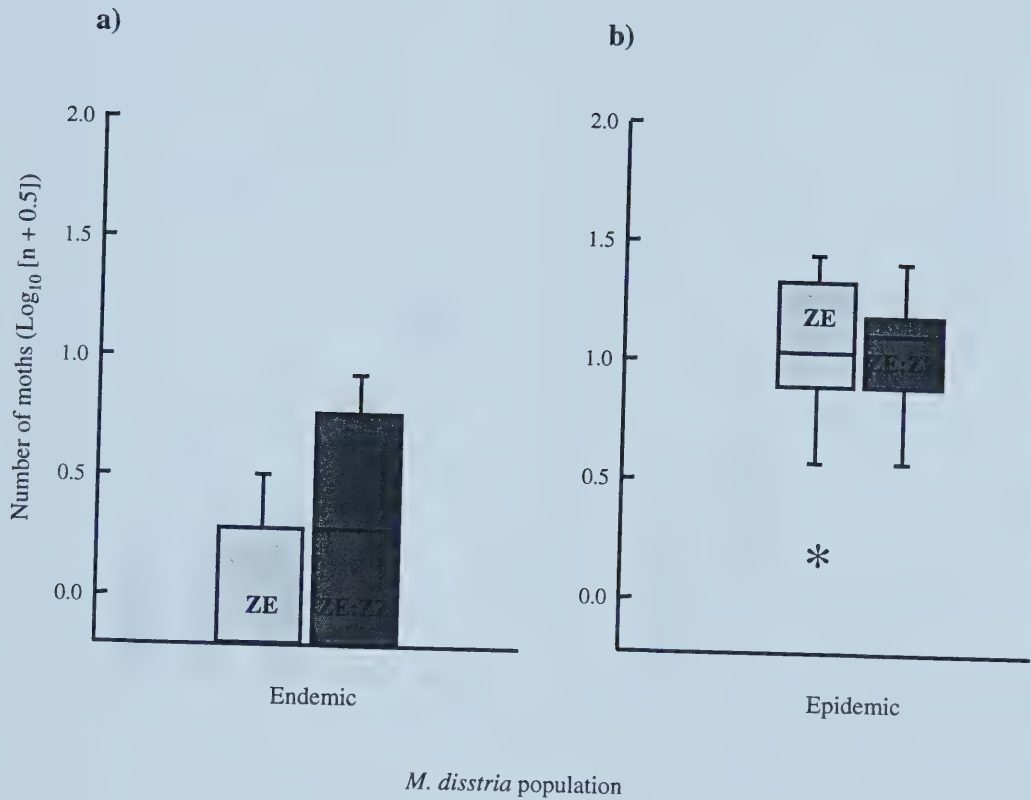


Figure 2.3: Number of *M. disstria* caught (box and whisker plots) using ZE-only and ZE:ZZ pheromone blends at **a)** endemic (Ministik Hills) and **b)** epidemic (Prince George) population levels. Pheromone abbreviations are defined in Table 2.1. Trap catch is significantly different at the endemic sites (Mann-Whitney $U = 314.5$, d.f. = 1, $n = 21$, $p = 0.01$), but not at the epidemic sites (Mann-Whitney $U = 199.5$, d.f. = 1, $n = 20$, $p = 0.989$). Plots as defined in Fig. 2.2.

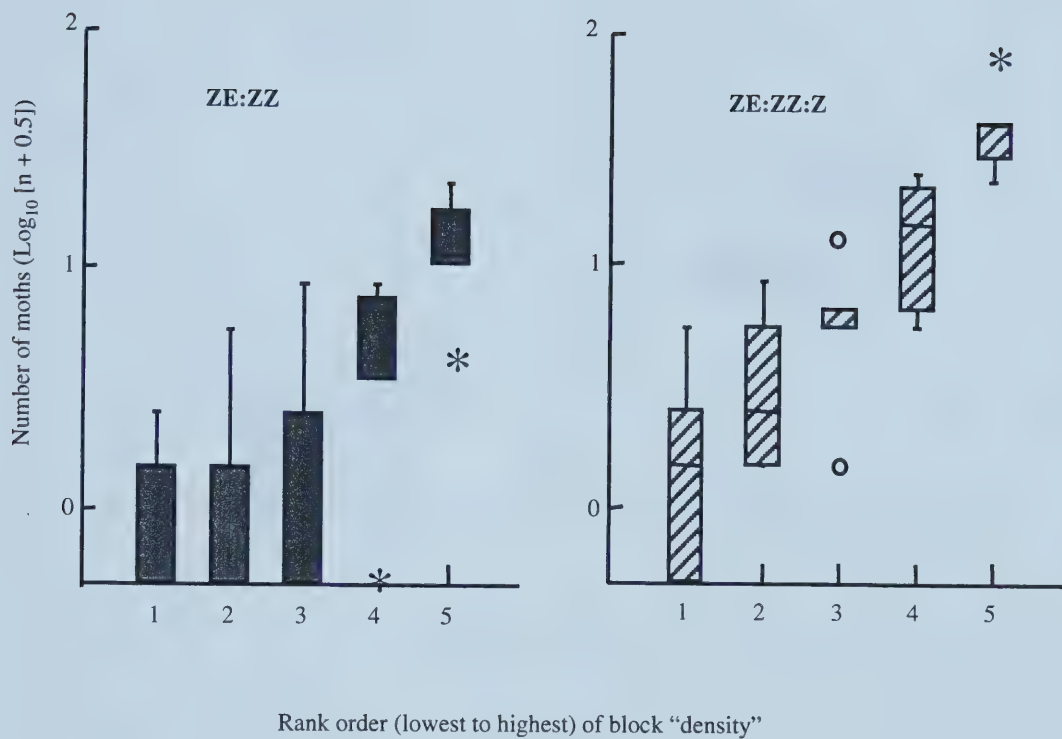


Figure 2.4: Number of *M. dissstria* caught (box and whisker plot) using **a)** the ZE:ZZ pheromone blend and **b)** the ZE:ZZ:Z blend. Plots as defined in Figure 2.2.

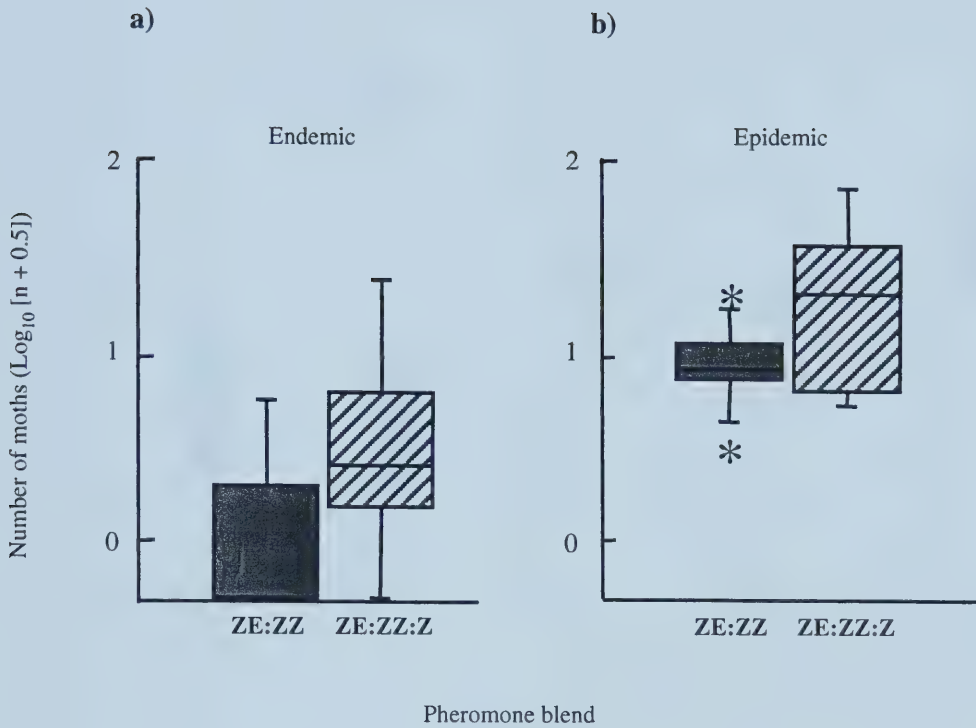


Figure 2.5: Number of *M. disstria* caught (box and whisker plots) using the ZE:ZZ and ZE:ZZ:Z pheromone blends, at endemic (a) and epidemic (b) population levels. Trap catch is significantly different at the endemic sites (Mann-Whitney $U = 50.5$, d.f. = 1, $n = 15$, $p < 0.01$), but not at the epidemic sites (Mann-Whitney $U = 28.0$, d.f. = 1, $n = 10$, $p > 0.05$). Pheromone abbreviations are defined in Table 2.1 and plots are as explained in Figure 2.2.

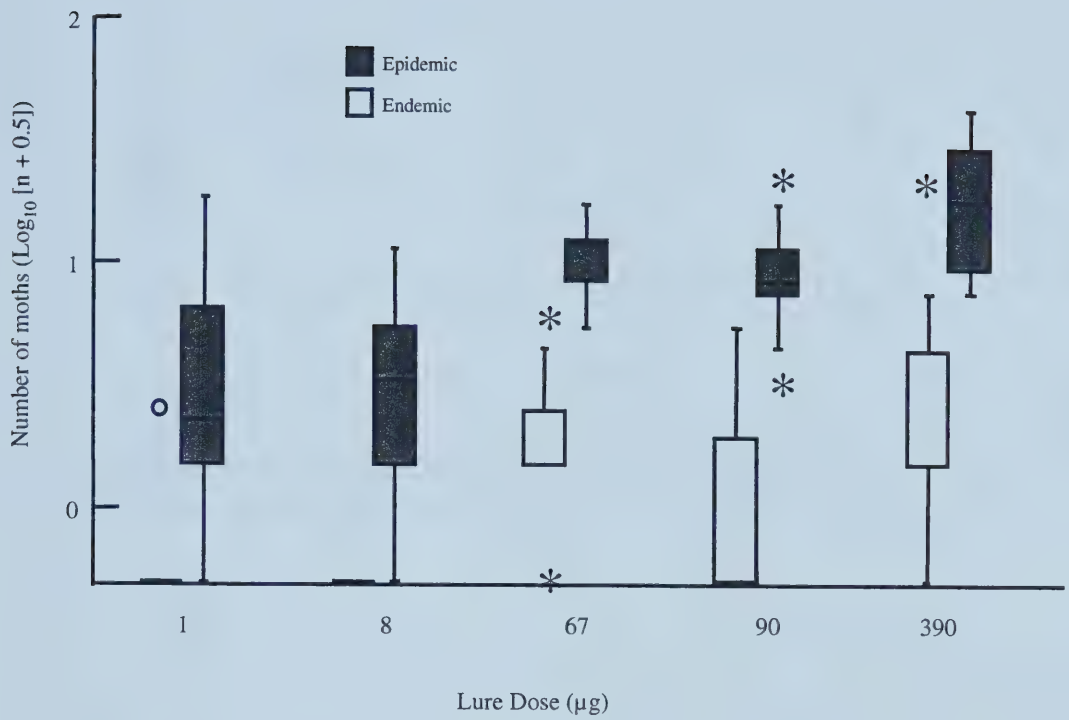


Figure 2.6: Number of *M. disstria* caught (box and whisker plots) using lure dosages between 1 µg and 390 µg of ZE:ZZ pheromone (see Table 2.1 for pheromone constituents). Plots are as explained in Figure 2.2.

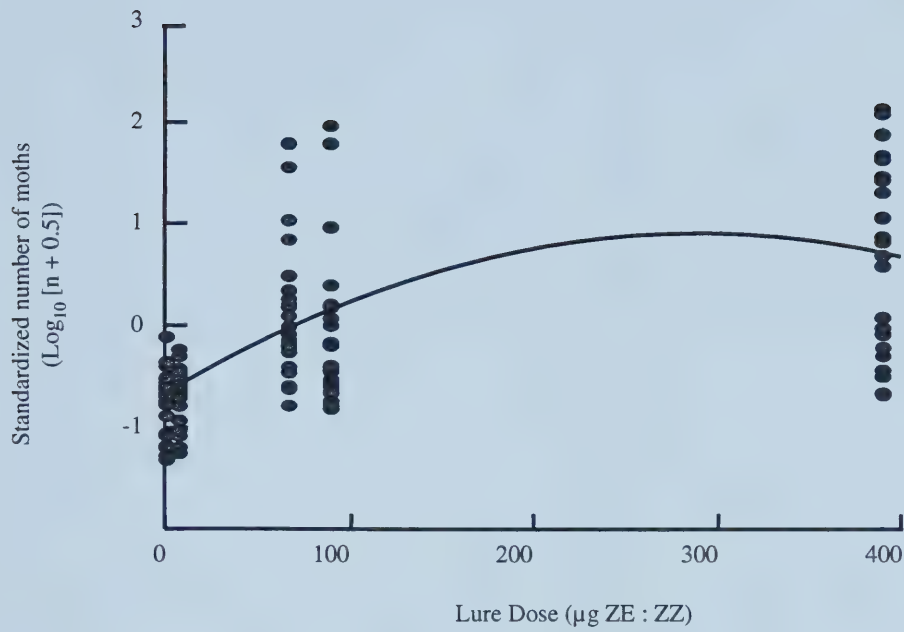


Figure 2.7: Trap catch of *M. disstria* as a function of ZE:ZZ pheromone lure dose. $Y = 9.82 + 5.22X - 2.38X^2$. Pheromone constituents are defined in Table 2.1.

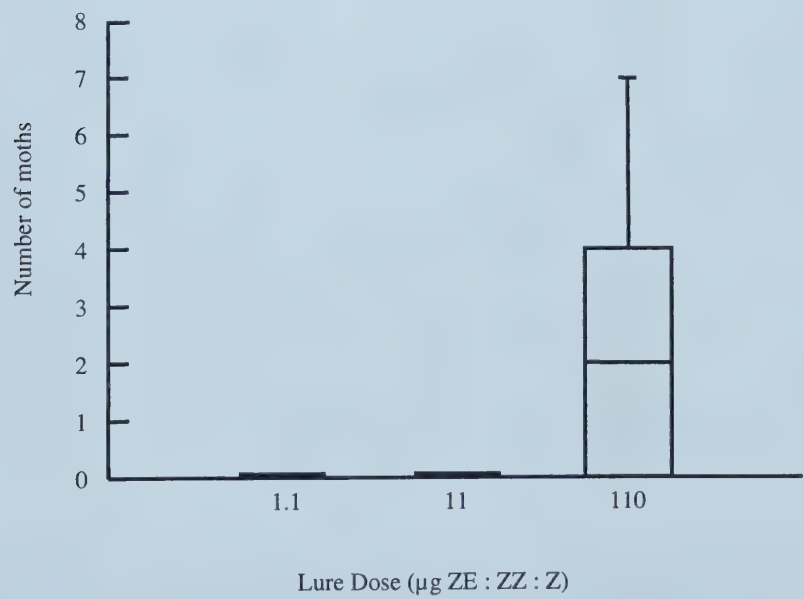


Figure 2.8: Number of *M. disstria* caught (box and whisker plots) at endemic sites, using 1.1μg, 11μg, and 110μg lure loads of ZE:ZZ:Z. Pheromone constituents are defined in Table 2.1 and plots are as explained in Figure 2.2.

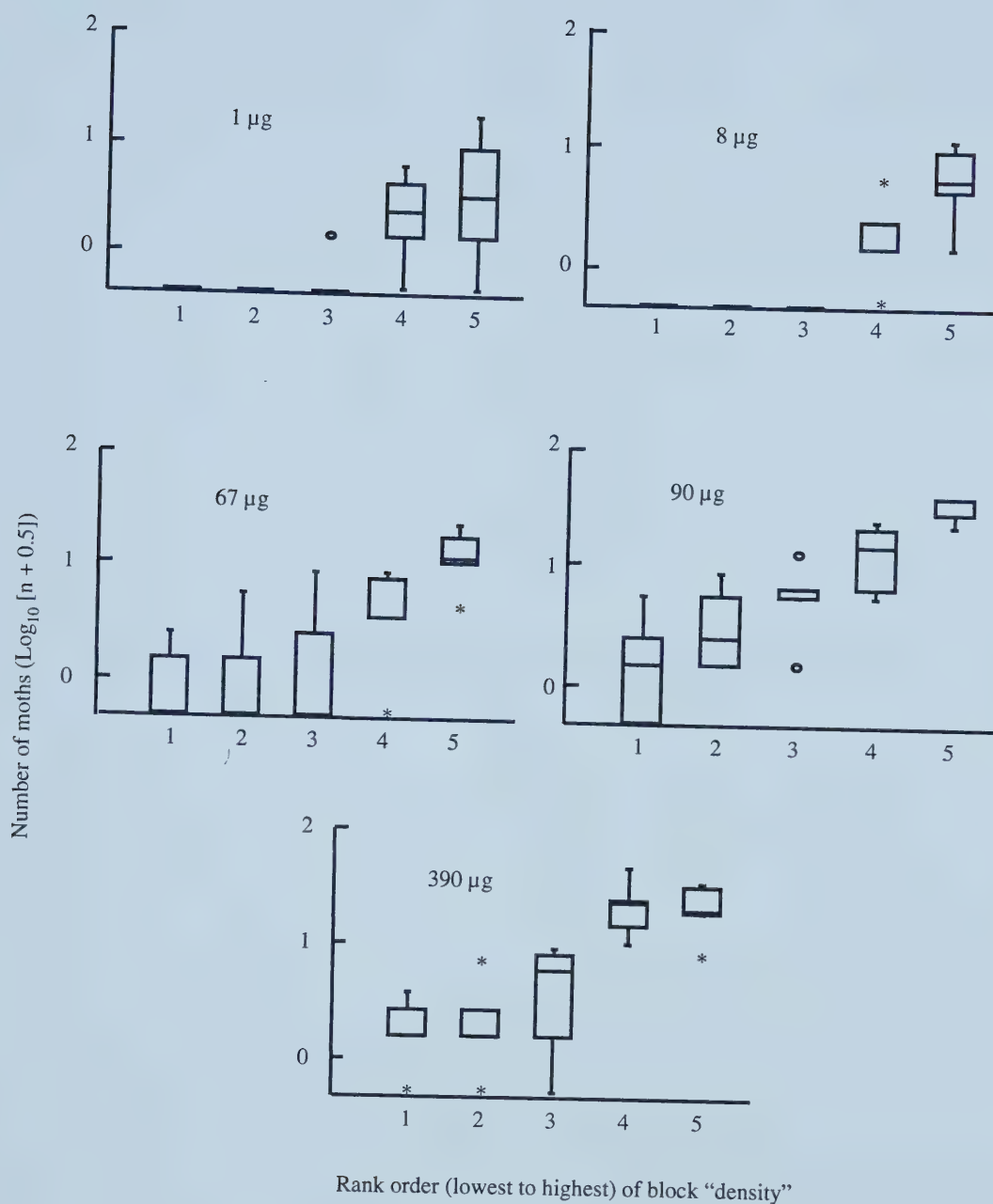


Figure 2.9: Number of *M. disstria* caught among sites ranked according to overall *M. disstria* density, for each lure dose of the ZE:ZZ pheromone blend. $N = 5$ for each combination of density and load treatment. Pheromone constituents are defined in Table 2.1 and plots are as explained in Figure 2.2.

Chapter 3

IMPROVED TECHNIQUES FOR MONITORING FOREST TENT CATERPILLAR POPULATIONS USING SYNTHETIC PHEROMONES.

INTRODUCTION

Populations of the forest tent caterpillar (FTC), *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) are well known for their periodic outbreaks and large fluctuations in abundance (Sippell 1957). Outbreaks often result in reduced growth and dieback of the FTC's primary larval host, trembling aspen (*Populus tremuloides*) (Churchill *et al.* 1964, Pendrel, 1991). The increase in value of aspen began in the late 1980s (Bryson 1989), which has been paralleled by a greater interest in insects and diseases affecting aspen. Predicting FTC outbreaks and monitoring their widely fluctuating populations for managing aspen harvest regimes has therefore become desirable. In addition to benefits to forest pest management strategies for FTC, the large body of research on FTC population dynamics has been limited to studies conducted in high-density or collapsing FTC populations (e.g. Myers & Kukan 1995, Roland & Taylor 1997. See (Otvos *et al.* [1998] for a complete bibliography), because monitoring techniques such as pheromone trapping that are sensitive to low-density populations are not available for the FTC.

Sex pheromone traps have considerable potential as monitoring tools for the FTC. This study addresses a number of factors known to affect trap efficacy, which are therefore important in developing an optimum pheromone trapping system. The variables tested in this study include pheromone dispenser (lure) type, lure age, and trap design.

Specifically, field experiments were conducted to: 1) compare the performance of rubber septa to polyethylene tube lures, 2) identify lure longevity, and 3) compare the performance of sticky-type to high-capacity pheromone traps. Capture data using a single

trapping technique such as pheromones may yield misleading results (Muirhead-Thompson 1991), and pheromone trap catch was therefore also compared to light trap catch.

METHODS AND MATERIALS

Study Sites

Field experiments were carried out in two areas between 1998 and 2000, one of outbreak FTC densities in central British Columbia and one of endemic (non-outbreak) FTC densities in central Alberta. The Prince George, BC and Ministik Hills, AB sites are described in detail in Chapter 2. In addition to the Ministik Hills site, I also conducted field trials testing the effect of lure age on trap efficacy in and adjacent to the Redwater Natural Area (53E55' N 112E57' W), approximately 50 km northeast of Edmonton, Alberta. The Ministik Hills site had very low FTC densities in 1999, so the Redwater site was subsequently chosen to conduct trials at the slightly higher FTC abundance levels present there (C. Schmidt, unpublished data). The terrain at the Redwater Natural Area consists of stabilized sand dunes, and is characterized by a mix of upland and wetland vegetation. Open jack pine (*Pinus banksiana*) forest is interspersed with stands of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black spruce (*Picea mariana*). Green alder (*Alnus crispa*), willow (*Salix* spp.) and wild rose (*Rosa* spp.) were common understory shrub species.

Pheromone dispensers

I evaluated the field performance of two pheromone dispenser types, the commonly used rubber septum (Datterman 1982) and a polyurethane dispenser (Flex Lure). The red rubber septa were obtained from Phero Tech Inc., Delta, BC. The Flex Lure, manufactured by and obtained from Phero Tech Inc. (Delta, BC), consists of 5 mm open-ended polyvinylchloride tubing filled with polyurethane. The active ingredient used in these lures was a two-component aldehyde blend, consisting of 100:1 (5Z,7E) 5,7 dodecadial : (5Z,7Z) 5,7 dodecadial (Chisholm *et al.* 1983; see also Chapter 2) at concentrations of 67 µg per lure. Lures were placed inside Wing Traps (Fig. 3.1) obtained from Phero Tech Inc., Delta BC. Traps were deployed at outbreak (Prince George, BC) and endemic (Ministik Hills, AB) FTC population densities, and placed out in a randomized block configuration consisting of three treatments per block: the two "lure types" discussed here, in addition to a "pheromone blend" treatment (Chapter 2). The traps were spaced at 50 m, and were suspended from tree branches between 1.5 m and 2 m above ground level. Traps were left out over an interval from early July 1998 prior to the onset of the FTC flight period until the end of August.

Statistical Analysis

I compared mean trap catch between treatments separately for the outbreak and endemic FTC populations. Because log-transformation failed to adequately normalize the distribution of the count data, I used non-parametric methods (Zar 1999) to compare the two treatments. Mean trap catches were compared using a Mann-Whitney test for the outbreak-level data, and a Wilcoxon paired-sample test for the endemic population data

since pairing was not recorded for these sites. To test whether or not the frequency of zero-catches was equal between traps baited with rubber septa and Flex Lures, I calculated a Chi-squared test statistic based on a 2 x 2 contingency table with one fixed margin (Zar 1999).

Lure longevity

I tested the longevity of the Flex Lure pheromone dispenser under field conditions, using the two-component aldehyde described above as an active ingredient. Lures loaded with 95 µg of pheromone were tested using the Universal Moth Trap (= Uni-trap, Figure 3.2). Because trap colour is known to affect trap performance (Hendricks & Calcote [1991], and references therein), green trap components were selected. A 2.5 cm x 4.5 cm piece of Hercon[®] Vaportape II, an insecticidal strip containing 10% dichlorvos (2,2-dichlorovinyl dimethyl phosphate), was placed in the traps as a killing agent. Fourteen traps were placed out at 7-day intervals at the Redwater study site, with the first replicates set out on 26 June 2000. This resulted in lures field-aged for 0d, 7d, 14d, 21d, and 28d by late July, near the peak of adult FTC activity (Fig. 3.6). The amount of time I was able to age lures was limited by the late arrival of the lure shipment. Lures were stored at 10°C in sealed plastic bags prior to deployment in the field. The few moths that had been caught in the traps prior to the deployment of unaged traps were removed. Traps were placed within 5 m of the forest edge at 100 m intervals along Township Road 572 and Range Road 205, in and adjacent to the Redwater Natural Area. The five age treatments were randomized within 14 blocks.

To compare lure longevity to the phenology of FTC adults in Alberta, I compiled historical records of pinned FTC moths. Label data were compiled from specimens in the University of Alberta Strickland Museum and the Northern Forestry Centre (Canadian Forest Service, Edmonton). I did not include reared adults, since these may not reflect development under ambient climate conditions that could result in anomalous emergence dates.

Statistical analysis

To compare trap catch among lure age treatments, I performed a non-parametric analysis of variance (Zar 1999). Because the overall trap catch was low (mean = 1.10 moths / trap, S.E. = 0.16) and five treatments were being compared simultaneously, I also compared 0d- and 28d-old lures separately, because this provides a statistically more powerful means by which to test the effect of lure age on trap catch.

Trap type

Three trap designs widely used for monitoring lepidopteran pests were evaluated for FTC trapping efficacy. The trap types tested included a sticky pheromone trap (Wing Trap), a high capacity pheromone trap (Uni-trap), and an ultraviolet light trap. The Wing Trap consists of a plasticized cardboard bottom tray with a 15 x 13 cm sticky surface, which fits tightly to a 23 x 28 cm cover from which the lure is suspended (Fig. 3.1). Two entrances for moths are found at either side of the trap (Fig 3.1). The Universal Moth Trap, or Uni-trap, is a plastic bucket-and-funnel design (Fig. 3.2). Uni-trap components are available in a variety of colours, and the components used in this study were green.

Light trapping was conducted using 12-watt DC ultraviolet light traps (BioQuip Products, Gardena, CA). These were deployed at dusk and operated until sunrise using 12 volt, 7 Amp-hour rechargeable batteries (Global & Yuasa Battery Co., Korea). Hercon[®] Vaportape II, described above, was used as a killing agent in the Uni-traps and light traps. Ethyl acetate was also used as a rapid knockdown agent in the light traps. A 250 ml Nalgene[®] bottle containing ethyl acetate with a 4 cm x 4 cm x 15 cm sponge wick was placed in each trap.

To compare trap performance in endemic FTC populations, fourteen replicates of each pheromone trap type were alternately placed at 100 m intervals, suspended at a height of 1.5 m - 2 m above ground. I avoided hanging traps directly adjacent to tree boles to allow relatively unobstructed pheromone plume dispersion. This study was carried out during July and August of 2000 at the Ministik study site. As part of a separate study, Wing Traps were deployed at the Prince George site (Chapter 2) in 1998, which was experiencing a FTC outbreak. Wing Trap capacity was estimated visually from these samples.

Data comparing Uni-trap catch (J. Roland, unpublished data) and light trap catch (Chapter 4) were collected in 1999 and 2000. These studies were conducted in the Ministik Hills at 12 sites in 1999, with an additional 6 sites in 2000. Sites adjacent to one another were at least 1.6 km apart, and each site received two Uni-traps spaced 50 m apart, with one light trap 20 - 100 m from the nearest pheromone trap. The pheromone

traps operated continually over the FTC flight period, whereas the light traps operated approximately once every seven days.

To estimate the mean number of moths caught / light trap / day, I averaged the total number of FTC caught during the sampling period by the number of nights that at least one moth was recorded among combined catches for all sites. The average daily pheromone trap catch was based on mean total catch / trap averaged over the FTC flight period. The length of the flight period was defined as the number of days between the first and last FTC occurrence in light trap samples (Fig. 3.6).

Statistical analysis

Trap catches comparing the Uni-trap to the Wing Trap were analyzed using the Mann-Whitney test (Zar 1999). To test whether or not the proportion of zero-catches was equal between Uni-traps and Wing Traps, and between Uni-traps and light traps, I calculated a Chi-squared test statistic based on a 2 x 2 contingency table with one fixed margin (Zar 1999).

RESULTS

Pheromone dispensers

At endemic FTC densities, captures of FTC males were significantly higher for traps baited with Flex Lure than traps baited with rubber septa (Fig. 3.3a); the mean number of moths captured was approximately ten times greater for traps baited with Flex Lure than those baited with rubber septa. Rubber septa trap samples had a significantly higher

frequency of zero-catches than did the Flex Lure Traps (Table 3.1). When tested in outbreak FTC populations, there was no significant difference in trap catch between the Flex Lure and rubber septa traps (Fig. 3.3b). This lack of 'lure type' effect at high FTC densities was likely due to the saturation of the Wing Trap sticky surface by FTC moths (see 'Trap design' below). All traps caught at least one moth at outbreak densities, precluding comparison of zero-catch frequencies.

Lure longevity

The number of FTC moths captured did not differ significantly among age treatments of the Flex Lure (Fig. 3.4). Because mean trap catch was low (1.1 moths / trap), and five treatment categories were compared simultaneously, I also compared the trap catch between the 28-day and zero-day lures to increase the power of the statistical test to detect a difference in catch. Again, there was no significant difference in trap catch between the 28d and 0d-old lures (Mann-Whitney $U = 84$, d.f. = 1, $p > 0.05$).

Capture dates of FTC moths from historical records ranged from 22 June to 21 August, with 91% of the records occurring from 1 July through 10 August (Fig. 3.5). The peak in adult flight activity occurred between 11 – 20 July. Light trap data indicate that FTC moth abundance at Ministik Hills during 1999 and 2000 peaked between 22 July – 4 August, and 11 July – 2 August, respectively (Fig. 3.6). FTC moths were recorded over a longer period in 1999 (23d) than in 2000 (15d); this was possibly due to the greater abundance of FTC in 1999, which would result in a greater probability of FTC captures on a given day. Historical phenology data show longer flight duration and an earlier

abundance peak than do my light trap catches. This difference reflects annual and geographical variation in FTC phenology, and shows that the length of the FTC flight period is shorter in a given year than multi-year data would suggest. To maintain uniformity in trapping effort, it is therefore best to consider lure longevity in light of multi-year flight period means rather than annual phenology estimates.

Trap design

Wing Traps set out at the FTC outbreak site reached the holding capacity of moths, because the sticky surface became completely covered with moths, wing scales and hairs. Wing trap capacity was visually estimated to be between 20 and 25 FTC moths, based on the absence of functional sticky surface area remaining. Functional saturation of traps likely masked the effects of the 'dispenser type' treatment at high densities (Fig. 3.3).

At endemic FTC densities, trap catch in the Uni-trap was about twice as great as that for the Wing Trap (Fig. 3.7). The proportion of traps with zero-catches was higher for the Wing Traps than for Uni-traps, but not significantly so (Table 3.2). Average daily trap catch was significantly higher for the light traps than for the Uni-traps, with the Uni-trap capturing only about 2% of the mean daily light trap catch. However, the frequency of zero-catches was not significantly different among trap types in either 1999 or 2000 ($X^2 = 0.00$, d.f. = 1, $p > 0.98$, and $X^2 = 0.12$, d.f. = 1, $p > 0.50$) (Table 3.3). The number of FTC captured in light traps was more variable compared to pheromone traps, more so in 1999 than in 2000 (Table 3.3). For these reasons, the Uni-trap is superior to UV light traps for monitoring FTC populations (see below).

DISCUSSION

Many published studies have measured pheromone trap effectiveness by the number of insects captured (e.g. Lewis & Macauley 1976, Vincent *et al.* 1993, Lopez 1998). When traps are used to estimate insect density, however, the important criterion is not the number of insects caught, but how accurate density estimates are. In order to achieve accurate population estimates, traps should be able to capture insects at the lowest population density, have consistent efficiency from year to year, have the capability to hold trapped insects without becoming saturated, and exhibit low catch variability (all else being equal). In an effort to develop an optimum pheromone trapping system for the forest tent caterpillar, I evaluated the effects of lure substrate, trap design and lure age using a synthetic pheromone (100:1 [5Z,7E] 5,7 dodecadienal : [5Z,7Z] 5,7 dodecadienal) formulated to effectively monitor FTC populations (Chapter 2).

The Flex Lure pheromone dispenser caught more FTC moths and had lower zero-catch rates than the rubber septum at endemic FTC densities. The difference in capture rates due to dispenser type was not evident in outbreak FTC populations, likely attributable to the functional saturation of the trap sticky surface by FTC moths, which would have masked any treatment effects on trap catch. Differences in catch rates between the two dispensers can be explained by their respective pheromone release rates over time. The release rate of the rubber septum decreases exponentially over time (Butler & McDonough 1981), and its attractiveness to FTC males therefore decreases rapidly. Polyurethane lures, which exhibit a gradual decrease in release rate much like

polyethylene lures (McDonough *et al.* 1992), would maintain their attractiveness longer. The half-life of active ingredients on rubber septa depends on the volatility of the compounds involved (Butler & McDonough 1981). The half-lives of 12-carbon di-unsaturated aldehydes on rubber septa, such as those used in this study, are not known. However, Heath *et al.* (1986) reported half-lives for mono-unsaturated and saturated aldehydes, including that of (Z)-9-tetradecanal, a mono-unsaturated 14-carbon aldehyde with a half-life of 43d. Because both unsaturation and decreasing carbon chain length exponentially diminish the half-life of aldehydes (Heath *et al.* 1986), a 12-carbon di-unsaturated aldehyde would be expected to have a half-life substantially less than that of (Z)-9-tetradecanal. Given that the flight period of FTC spans less than 30d (Fig. 3.6), and that traps are deployed prior to the onset of the flight period, rubber septa likely become unattractive to FTC males before the end of FTC adult activity. Trap catch resulting from the use of rubber septa may therefore lead to inconsistent population estimates.

Field aging Flex Lures did not affect FTC trap catch. Lures provided a constant catch rate over a period of 28d. Because the FTC flight period at a given locality is approximately 30d, traps deployed shortly before the onset of FTC moth emergence should provide a constant rate of pheromone emission throughout the emergence period. Flex Lure pheromone dispensers should then also provide uniform year to year FTC trapping efficiency.

There is some evidence suggesting that sticky traps have higher capture rates at low target insect densities than non-saturating traps (Elkinton & Childs 1983, Angerilli &

McLean 1984). In this study, the sticky Wing Trap proved to be less suitable for trapping male FTC than the high-capacity Uni-trap at both high and low FTC population levels. At epidemic FTC levels, wing traps saturate and become ineffective. The efficiency of sticky traps also decreases prior to the saturating point as moths accumulate on the sticky surface (Daterman 1982). Wing Trap saturation occurs at approximately 20 FTC moths per trap, or $0.1 \text{ moths} / \text{cm}^2$ of sticky surface (C. Schmidt, unpublished data). Sheperd *et al.* (1985) found that delta-type sticky traps became saturated with Douglas-fir tussock moths (*Orgyia pseudotsugata*) at approximately $0.06 \text{ moths} / \text{cm}^2$. Given that the Douglas-fir tussock moth has a slightly larger wing area (Ferguson 1978), which would lower the saturation point, trap saturation is comparable between these two species.

The ability to detect the presence of FTC at a given site was similar for pheromone-baited Uni-traps and light traps. Pheromone- and light-traps attract moths for very different reasons, and the large difference in trap catch could be due to many factors. The relatively smaller size of pheromone traps may mean that they are less efficient at capturing moths than are light traps, and the catchment area (the area from which moths are attracted) may differ depending on trap and attractant type. Directionality of the attractant source also differs between trap types, with light being emitted over 360° , whereas pheromone is only attractive downwind from the source. Although light traps capture both sexes of FTC, only one female was recorded in the data presented here, so this does not help explain catch differences. Intuitively, the daily activity pattern of FTC moths may also affect trap catch. Although the emission of pheromone is continuous throughout the day using lure traps, there is some evidence to suggest that FTC males

only respond to pheromones for several hours every day (Shepherd 1979). Pheromone traps may therefore only be actively attracting males over a short (3 - 4h) period. In contrast, FTC moths can be drawn to light during an extended flight activity period between sunset and sunrise (Schmidt & Roland 2001). The greater light trap catch of FTC in comparison to pheromone trap catch is consistent with results obtained for the European corn borer (Kennedy & Anderson 1980), although several studies have shown that pheromone traps are more effective than light traps (Campbell *et al.* 1992, Lee *et al.* 1993, Shih & Chu 1995, Kim *et al.* 1995).

Although light traps had a higher capture rate than did Uni-traps, light trap catch was also more variable. Light traps are more sensitive to weather and site conditions (Bowden 1982), and this could cause higher variation in catch between sites than for pheromone traps. Since uniformity of population estimate efforts between years is the most important factor in long-term monitoring of pest species (Sanders 1986a), and the logistics and cost of light traps precludes large-scale monitoring, a non-saturating trap design such as the Uni-trap should be used as part of the FTC monitoring protocol.

At endemic FTC population levels, the Uni-trap had a greater ability to estimate FTC abundance compared to the Wing Trap, since average trap catch was higher and the frequency of zero-catches was slightly lower. It appears, therefore, that Uni-traps are more efficient at capturing moths, i.e. more moths are attracted to the trap due to pheromone plume characteristics and/or there are fewer 'escapees'; the open, circular design of the Uni-trap allows omni-directional dispersal of the pheromone scent plume,

as opposed to the Wing Trap which is open to air movement from only the two ends. In FTC outbreaks, the Uni-trap should also provide more accurate FTC population estimates than sticky traps because they have a much greater functional saturation point. Given the favorable performance of the Uni-trap and Flex Lure, this trapping system, used in conjunction with 100:1:10 (5Z,7E) 5,7 dodecadienal : (5Z,7Z) 5,7 dodecadienal : Z,7 dodecanal as an active ingredient, provides the basis for an optimal FTC monitoring protocol.

Further research

Further work should be directed towards developing the trapping system presented here as a predictive tool of FTC outbreaks. Attempts should be made to correlate trap catch to larval population density (Shepherd *et al.* 1985) to establish trap catch levels indicative of incipient outbreaks. Depending on the desired precision of FTC population estimates, the number of trap replicates per site, trap spacing and configuration should also be investigated, because these factors all influence precision of population estimates (Shepherd *et al.* 1985).

It would also be desirable to determine the effects of trap colour, as this has been shown to affect efficiency of Uni-traps for other species (Hendricks & Calcote 1991, Lopez 1998). Multi-coloured Uni-traps are generally more efficient, presumably because they present a visual stimulant to males engaged in mate-searching behaviour. Male FTC searching for females respond to objects similar in size and colour to FTC moths

(Palaniswamy *et al.* 1980), so visual stimulus is apparently an important factor in mate location for the forest tent caterpillar.

Some lepidopteran species are repelled slightly by the insecticidal strip (DDVP) used in the Uni-traps during this study (Sanders 1986b), while other species are unaffected by DDVP (Lindgren *et al.* 1984). The effects of DDVP on the attractiveness of traps to FTC are not known. The fact that Wing Traps without DDVP were less effective than Uni-traps with DDVP suggests that this insecticide does not appreciably repel FTC moths. Care should be taken to ensure similar amounts of insecticide are used in traps to provide consistent trapping effort, should DDVP prove to adversely affect FTC response to pheromone traps. Sanders (1986b) also showed that dead insects, including target species, accumulated in high capacity traps could reduce the captures of spruce budworm (*Choristoneura fumiferana*). Whether this phenomenon occurs in the FTC trapping system is not known.

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Zar, J.H. 1999. Biostatistical Analysis (Fourth Edition). Prentice Hall, Upper Saddle River, New Jersey.

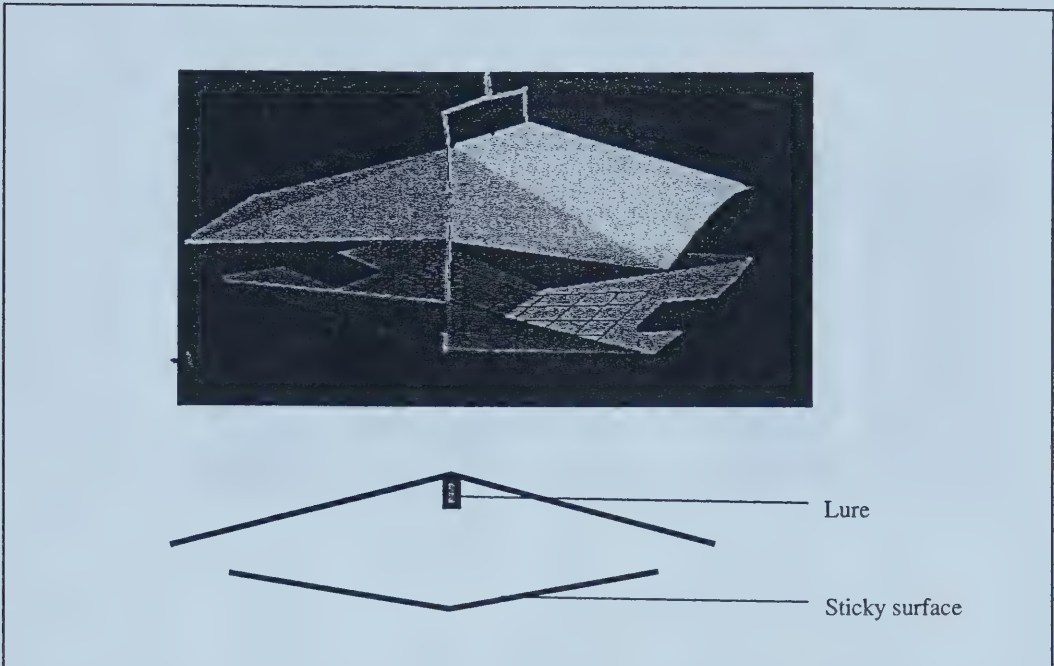


Figure 3.1: Wing trap, with longitudinal cross-section (**bottom**) to show placement of pheromone lure. The bottom tray is lowered to show the sticky surface, indicated by the grid pattern.

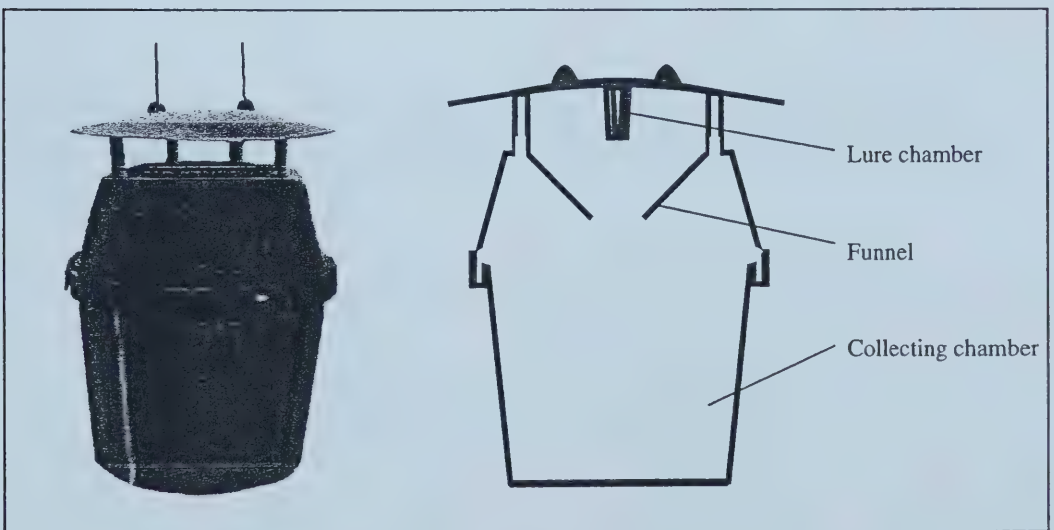


Figure 3.2: Universal Moth Trap (Uni-trap), with cross-sectional view (right) to show lure chamber and funnel.

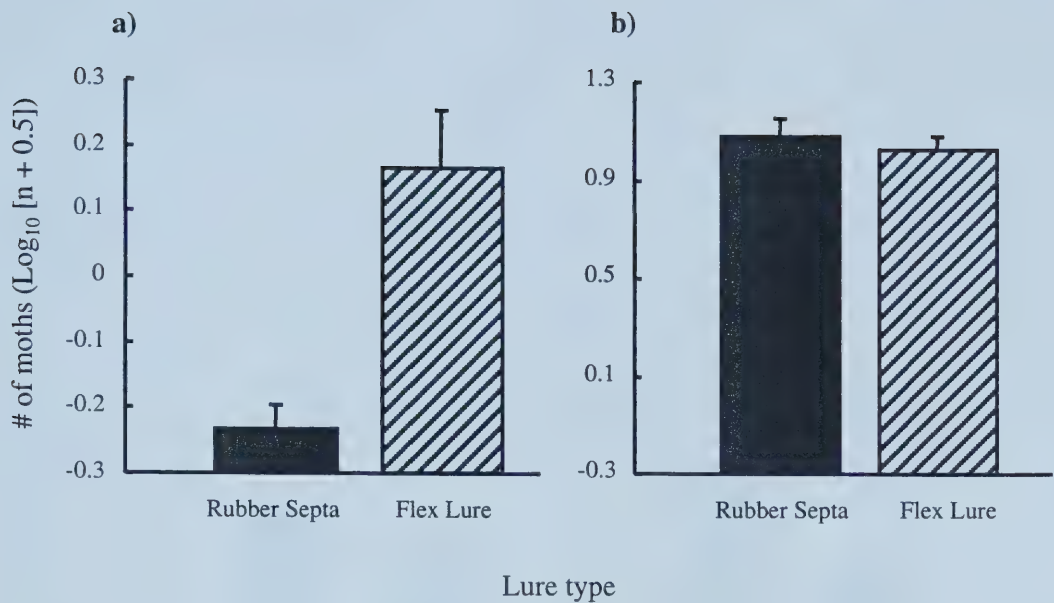


Figure 3.3: Trap catch in Wing Traps as a function of lure substrate at endemic (a) and outbreak (b) *M. disstria* densities. The number of *M. disstria* caught is significantly different between lure type at non-outbreak densities (Mann-Whitney $U = 96.0$, d.f. = 1, $p < 0.001$, $n = 21$), but not at outbreak densities (Wilcoxon paired-sample test, $T(-) = 85$, $p > 0.05$, $n = 20$).

Table 3.1: Frequency of zero-catches in rubber septa-baited traps and Flex Lure-baited traps at endemic *M. disstria* densities. Frequencies are significantly different ($X^2 = 9.88$, d.f. = 1, $p < 0.005$).

Trap catch	Lure type	
	Rubber septa	Flex Lure
0	18	7
>0	3	14
TOTAL	21	21

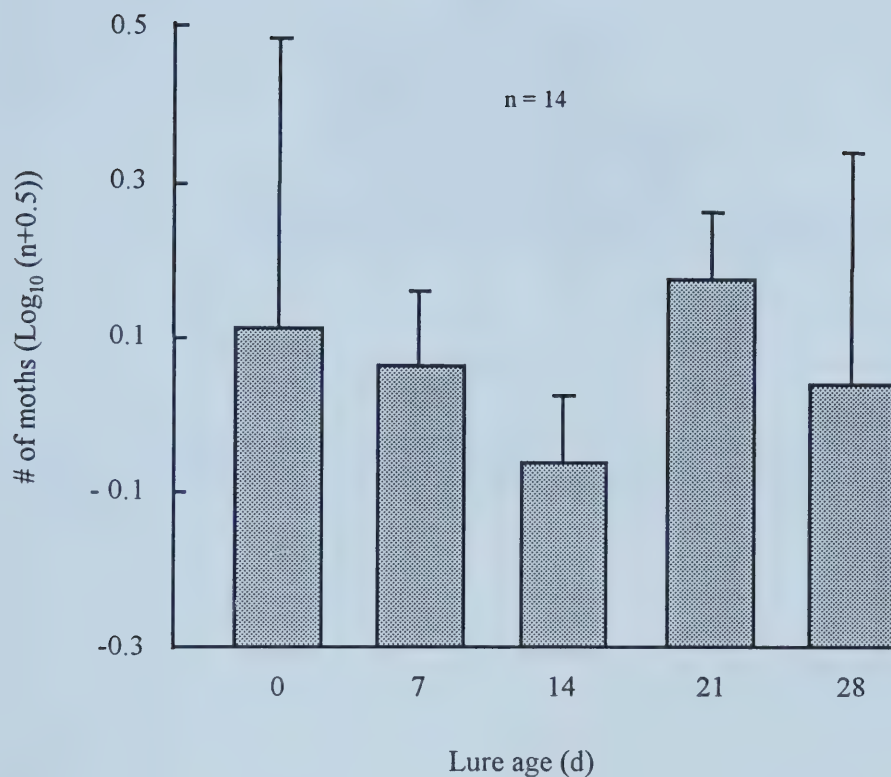


Figure 3.4: Number of *M. disstria* moths captured (+S.E.) as a function of lure age, when traps are deployed on the same date. Trap catch is not significantly different between lure age treatments (Kruskal-Wallis $H = 3.64$, d.f. = 4, $p = 0.46$).

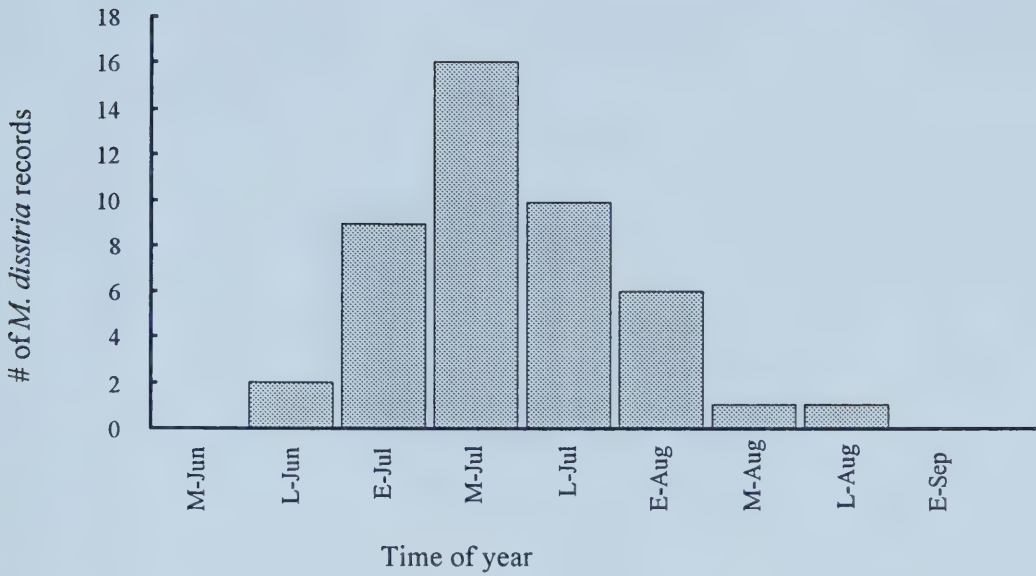


Figure 3.5: Seasonal distribution of *M. disstria* adults in Alberta. E(arly), M(id), L(ate) corresponds to the 1st - 10th, 11th - 20th, and 21st - last day of the month, respectively.

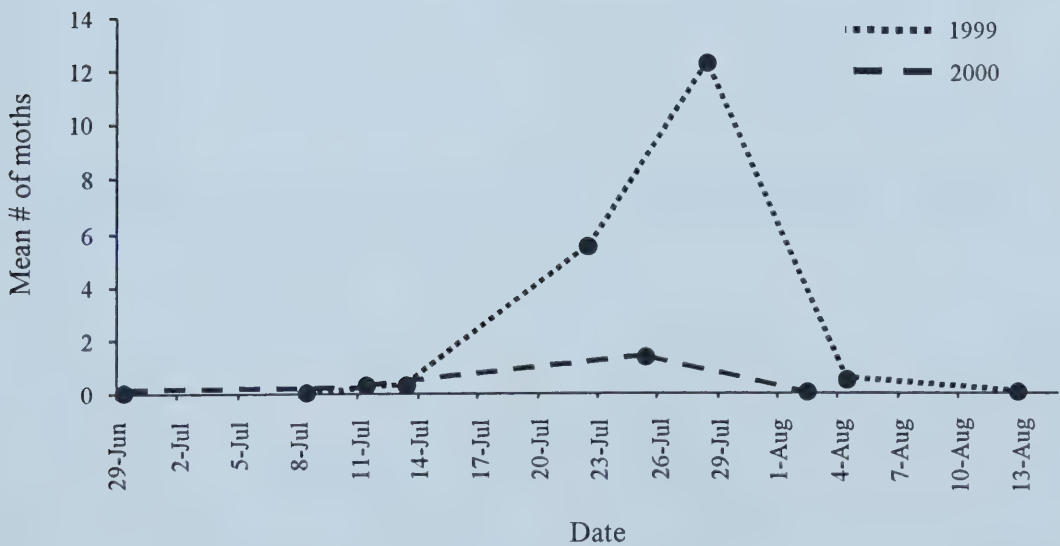


Figure 3.6: Light trap catch of *M. disstria* moths at Ministik Hills in 1999 (n = 12 traps) and 2000 (n = 24 traps).

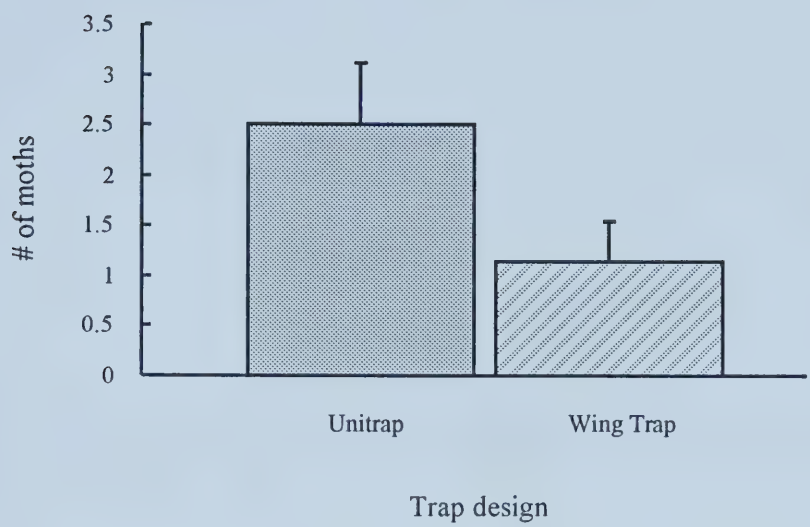


Figure 3.7: Comparison of the number of moths caught (+ S.E.) using the Unitrap and Wing Trap at low *M. disstria* population levels. Trap catch is significantly different ($T = 0$, $p < 0.001$, $n = 14$).

Table 3.2: Frequency of zero-catches using the Uni-trap and Wing Trap at endemic *M. disstria* densities. Frequencies are not significantly different ($\chi^2 = 0.16$, $p = 0.50$ d.f. = 1).

Trap catch	Trap type	
	Uni-trap	Wing Trap
0	4	6
>0	10	8
TOTAL	14	14

Table 3.3: Daily trap catch of *M. disstria* using light traps and Uni-traps at Ministik Hills in 1999 and 2000. The mean daily catch, standard error of the mean and coefficient of variation are given.

Trap Catch	Trap type			
	1999		2000	
	Light trap	Uni-trap	Light trap	Uni-trap
Mean	4.67	0.083	1.00	0.022
S.E.	1.35	0.016	0.30	0.005
C.V.	1.00	0.67	1.26	1.03
Zero-catch	0	1	6	8
N	12	12	18	18

CHAPTER 4

EFFECTS OF FOREST FRAGMENTATION ON THE HOST ASSEMBLAGES OF FOREST TENT CATERPILLAR PARASITIDS

INTRODUCTION

The forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae), is a widespread defoliator of forest trees throughout North America. Although the forest tent caterpillar (FTC) feeds on many species of deciduous trees and shrubs, the primary host plant throughout the boreal forest region is trembling aspen (*Populus tremuloides* Michx.). The FTC is one of the most dramatic examples of a cyclic pest species, with outbreak periodicity varying according to geographic location (Fitzgerald 1995). Natural enemies, such as predators, pathogens and parasitoids are the most important mortality factors in the population dynamics of the FTC, and are often thought to be responsible for causing outbreak collapse (Witter & Kulman 1972, Roland & Taylor 1995). In Alberta, five species of Dipteran and Hymenopteran parasitoids predominate in outbreak FTC populations, often causing over 70% mortality of caterpillars and pupae (Roland & Taylor 1995, Parry 1995). The outbreak phase of FTC's can vary from one to eight years, some of this variation being attributable to parasitoid efficacy mediated by forest structure (Roland & Taylor 1995). Population outbreaks of FTC last several years longer in forests that have been fragmented by agriculture and forestry, compared to shorter outbreaks in large, continuous forests (Roland 1993). At high FTC density, forest fragmentation reduces the impact of most mortality agents, such as parasitoids (Roland *et al.* 1996, Roland & Taylor 1997) and viral pathogens (Roland & Kaupp 1995, Rothman & Roland 1998).

Although FTC may be present at virtually undetectable levels for many years, almost all studies of FTC have been restricted to populations at moderate and high densities.

Harmsen & Rose (1983) compared early instar mortality between upland and lowland plots in an endemic population, but did not differentiate predator and parasitoid species. Parry (1994) investigated predation and parasitism of larval colonies placed out in a recently collapsed FTC population, and found that the greatest mortality rates resulted from avian predation on larvae and pupae. However, FTC population levels in this study were quantified based on the detection of egg masses, which, as discussed in Chapter 1, is an imprecise measure of endemic populations.

The role of parasitoids in regulating endemic (vs. epidemic and collapsing) FTC populations remains largely unknown. The relative importance of each parasitoid species varies through time during different stages of an outbreak (Sippell 1957, Witter & Kulman 1979, Parry 1995) and may be mediated by parasitoid host range, especially during the non-outbreak phase. Parasitoids that are able to prey on hosts other than FTC (those with broader host ranges) are at an advantage, since they are not vulnerable to extinction because of extremely low FTC densities. In contrast, those parasitoids that rely solely or primarily on FTC could go extinct locally because of spatial variation in FTC abundance. Several factors can induce localized spatial variation in caterpillar abundance; for example, early larval instars are more susceptible to the parasitoid *Aleiodes malacosomatos* (Mason) (Braconidae) in upland than in lowland forest stands (Harmsen & Rose 1983, Parry 1994). Furthermore, both elevation and microtopography affect winter egg mass survival through meteorological conditions (Cooke *in prep.*). As discussed above, forest structure at the regional scale can also influence the characteristics of a tent caterpillar outbreak. A shift in the parasitoid fauna from specialist

species in outbreak and collapsing populations to generalist species in endemic populations may exacerbate landscape structure effects by not only affecting parasitoids directly, but also indirectly through changes in the community structure of their hosts (Tscharntke 2000, Kruess & Tscharntke 2000).

Parasitoid polyphagy may therefore affect FTC population dynamics: the parasitoid's ability to maintain relatively higher densities during the FTC endemic phase (through density-dependent responses to prey other than FTC) would result in a more rapid numerical response as FTC abundance increases. Hence, the presence of alternate hosts would buffer parasitoid population fluctuations by preventing local extinctions (Hassell 1978, Latto & Hassell 1988).

This study examines the effects of forest fragmentation on an insect herbivore species assemblage, specifically the lepidopteran hosts of forest tent caterpillar parasitoids. My objectives were to 1) examine the host use patterns and relative host range breadth of the dominant forest tent caterpillar parasitoids, and 2) determine the effects forest fragmentation has on the abundance and diversity of parasitoid hosts. Based on these landscape-induced patterns, I then make several predictions of how this could affect the spatial and temporal characteristics of forest tent caterpillar population dynamics.

Ecology of FTC parasitoids

The biology of most FTC parasitoids remains poorly known, with the exception of a few ubiquitous species such as *Itoplectis conquisitor* (Say). The FTC parasitoid guild is dominated by five species during caterpillar outbreaks, namely *Leschenaultia exul*

(Townsend), *Patelloa pachypyga* (Aldrich & Weber), *Carcelia malacosomatos* Sellers, *Arachnidomyia aldrichi* (Parker) and *Aleiodes malacosomatos* (Mason). Dipteran parasitoids are the largest source of late-larval and pupal FTC mortality at high caterpillar densities. The tachinid flies *L. exul* and *P. pachypyga* attack during mid-larval stage, while the sarcophagid *A. aldrichi* parasitizes pupae and prepupae.

Tachinids exhibit four oviposition types (O'Hara 1985), two of which occur in the species attacking FTC. Several genera, such as *Chaetogena* and *Carcelia*, oviposit directly onto the integument of the host ('macrotype' eggs), whereas *Leschenaultia* and *Patelloa* oviposit 'microtype' eggs onto plant foliage in response to feeding damage by the host (Mondor & Roland 1997). Microtype eggs are ingested by the host, which then hatch and burrow through the digestive tract and develop in the body cavity (O'Hara 1985).

Tachinid larvae avoid encapsulation by posterior attachment to the trachea or through the integument, ensuring their air supply; this trait is thought to be important in the evolution of a relatively broad host range in the Tachinidae (Belshaw 1994), compared to the Hymenoptera. The Sarcophagidae are generally saprophytic (Shewell 1987), and *A. aldrichi* larviposits onto the host cocoon, upon which the larvae burrow into the pupa or prepupa.

Parasitic Hymenoptera that attack FTC develop inside the host (either in larvae or pupae) as a result of direct oviposition into the host stage attacked. *Aleiodes malacosomatos* is a koinobiont braconid wasp, meaning the host caterpillar continues to grow once it has

been parasitized (Shaw 1994). The ichneumonid species that attack FTC pupae are idiobiont endoparasites, with host development ceasing after parasitization (Shaw 1994).

Throughout this paper, I will use the term 'alternate hosts' to refer both to those hosts that are obligately used by multi-brooded FTC parasitoids, and those hosts that may be used facultatively by univoltine parasitoids.

METHODS AND MATERIALS

Parasitoid host range

To evaluate host use patterns of FTC parasitoids, I compiled host records from Arnaud's (1978) tachinid host catalogue, and from Krombein *et al.* (1979) for the Ichneumonidae. Additional records were obtained through literature searches (Table 4.2). Over 40 parasitoid species have been reared from FTC in the prairie region (Williams *et al.* 1996), and I have limited my analysis to the 17 species reported for Alberta (Parry 1995). Despite the possibility that some literature records of parasitoid hosts may be erroneous (Belshaw 1994), data on relative host range breadth is still informative (assuming error rates of host records are independent of the number of hosts for a given parasitoid species). Host range is examined in light of parasitoid biology, and the ecological characters of the hosts that are known to be related to host suitability in other host-parasitoid systems. The characters of potential hosts for FTC parasitoids include overwintering stage (phenology), larval morphology (smooth or hairy), gregariousness, host plant type, and host phylogeny (Sheehan 1994). Ecological characters of Lepidoptera were compiled from a number of sources including McGugan (1958),

Prentice (1962-1965), Stehr & Cook (1968), Ferguson (1978), Ferguson (1985), Scott (1986), Lafontaine (1987), Ives & Wong (1988), Tuskes *et al.* (1996), Wagner *et al.* (1997) and Handfield (1999). For each FTC parasitoid species, potential alternate hosts were assigned according to common unifying traits.

The reported host species of FTC parasitoids include a wide range of lepidopteran taxa. In order to compare this host assemblage to the North American fauna, I tabulated the proportion of species by family. The composition of the North American fauna was based on Hodges *et al.* (1983). Since there may be a sampling bias to certain lepidopteran groups for which parasitoids are known (for example, taxa popular with collectors, such as the Saturniidae, are relatively well-studied), I also compared the FTC parasitoid host assemblage to the macrolepidopteran hosts which have known tachinid parasitoids. I compiled all species that have at least one known tachinid parasitoid (Arnaud 1978). I limited this analysis to hosts that were identified to species with some degree of certainty; i.e. those identified only to genus were excluded, while those listed as "*Genus* probably *species*" were included only if no other parasitoid records for that species were given. Tachinids exhibit an extremely wide variety of ways in which hosts are attacked (Wood 1987), and this diversity of host use patterns is reflected in the diversity of hosts. I therefore made the assumption that tachinid hosts records should represent a random subsample of all the Macrolepidopteran taxa for which parasitoids have been recorded.

Study sites

Light trapping was carried out in the southern boreal forest of central Alberta, Canada during 1999 and 2000. The sampling grid covered a 20 km by 20 km area, centered on the Ministik Hills approximately 30 km east of the city of Edmonton (Figure 4.1). The Ministik Hills consist of gently rolling knob-and-kettle topography, and are located within the Cooking Lake Moraine. The surficial geology of the Cooking Lake Moraine consists of glacial till with a high clay content (Andriashek 1988). The Ministik Hills are within the dry boreal mixed wood ecoregion (Strong & Leggat 1992), and the natural vegetation is dominated by trembling aspen (*Populus tremuloides*) forest. Balsam poplar (*Populus balsamifera*) occurs as a dominant or co-dominant species in more mesic sites. Paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) occasionally form small, isolated stands. In upland sites, beaked hazel (*Corylus cornuta*) often forms a thick understory. Other common understory shrubs include red raspberry (*Rubus idaea*), red osier dogwood (*Cornus stolonifera*), Bebb's willow (*Salix bebbiana*) wild rose (*Rosa* spp.), saskatoon (*Amelanchier alnifolia*) and pin cherry (*Prunus pennsylvanica*). Wetlands, primarily sedge (*Carex* spp.) and cattail (*Typha latifolia*) marshes, are common throughout the study area. Non-forested land cover is largely the result of agricultural practices, primarily forage crops (hay and alfalfa) and pasture land for cattle grazing.

Forest fragmentation

The main components influencing abiotic and biotic conditions in forest fragments, as outlined by Andren (1994), are area effects, edge effects, fragment shape (edge : area

ratio), isolation, and connectivity. These components apply to all communities at the landscape level, although the relative importance of each is dependent upon the taxa in question and the nature of the landscape. Since the regional forest structure at Ministik Hills is more characteristic of perforation (*sensu* Hunter 1992) rather than discrete, isolated patches (Fig. 4.1), I used stand context (% non-forest vs. forest) as a surrogate measure of area and edge effects and connectivity for the purposes of this study. Forest structure was defined as the spatial context in which the study sites occurred, at scales between 200m and 600m. At the landscape scale, light trapping sites were selected to provide a range of surrounding forest (vs. non-forest) cover as a measure of forest fragmentation. The sites ranged from 20 - 90% fragmented (proportion of non-forest to forest) at three spatial scales (Table 4.1), measured in concentric circles with radii of 200m, 400m and 600m. Fragmentation was measured at varying scales since there were no *a priori* predictions for the scale at which moths would respond, and since response to fragmentation is known to be scale-dependent in other insects (Roland & Taylor 1997, Hamer & Hill 2000). Landscape structure was classified visually into forest and non-forest from 1:20,000 aerial photographs taken between 1994 and 1997. Landscape cover classified as non-forest included anthropogenic disturbances, water bodies, and wetlands. Subsequent forest cover parameters were calculated using "ImageTool for Windows 2.00" (UTHSCSA 1996). Twelve sites were sampled in 1999, with an additional 12 added in 2000. A minimum distance of 1.7 km separated sites from each other.

Because local topography can affect light trap catch (Waring 1994), trap locations with similar microtopography and surrounding vegetation structure were chosen. Traps were

located in upland sites at or near the top of the local topography (maximum relief within a 250m² area is approximately 10m). To minimize the effects of local vegetation on moth species composition, I also selected sites that were dominated by a beaked hazelnut understory.

Light trapping

Ultraviolet light traps (12 volt, 12-watt DC, BioQuip Products, Gardena, CA), operated using rechargeable, 7 amp-hour batteries (Global & Yuasa Battery Co., Korea), were used to sample moths at each of the sites. Traps were suspended from a piece of rope between two trees, between 1.5 and 2m above the ground. Traps were placed at least 3m from the nearest tree. To prevent the attraction of moths from adjacent open areas, sites were at least 20m from the nearest forest edge. The effective attraction distance of most UV-emitting lights to moths is between 3m - 10m (Baker & Sadovy 1978). Vegetation cover further prevented the light from being visible outside of the forest stand.

During 1999, all 12 sites were sampled on the same nights to control for the effect of meteorological conditions on trap catch (Morton *et al.* 1981). The 24 sites sampled in 2000 were split into two, 12-site grids and sampled on consecutive nights to minimize phenological and meteorological effects. Sampling was conducted approximately once every seven days, between mid May and early October (1999) and late May to early September (2000). Traps were not operated on cold nights, or on clear moonlit nights since trap catch is significantly lower under these conditions (Morton *et al.* 1981). Traps

were operated from dusk until dawn. Specimens were collected from the traps the following morning, and stored frozen in airtight containers until processed.

Taxonomic nomenclature and deposition of vouchers

Lepidopteran nomenclature follows that of Lafontaine *et al.* (2001) and Hodges *et al.* (1983). Nomenclature of the dipteran and hymenopteran parasitoids of FTC follows Williams *et al.* (1996). Moth species were identified using the available literature (e.g. Lafontaine 1997, 1998, McGuffin 1961-1988, Handfield 1999). The University of Alberta Strickland Museum reference collection and the private collection of Gary Anweiler (Edmonton) and my own collection were also used to help identify specimens. Only 'macrolepidopteran' species were recorded, comprised of the Drepanoidea, Geometroidea, Bombycoidea, Sphingoidea and Noctuoidea (Hodges *et al.* 1983); species in the families Hepialidae and Cossidae, which are generally grouped with the 'Microlepidoptera', were also included. Due to the difficulty in identification to species, the following macrolepidopteran taxa were excluded in 1999: Larentiinae (Geometridae), Sterrhinae (Geometridae), *Cabera* / *Protitame* (Geometridae) / *Eudeilinea* (Drepanidae), and *Euxoa* spp. (Noctuidae). All species, with the exception of the genus *Eupithecia* (Larentiinae), were recorded in 2000. Genitalic dissection is required to differentiate between several species-pairs, and these remain undifferentiated in the data set. In these situations, I dissected a limited number of specimens, which proved to be the more common of the two species. However, the presence of the second species (given in brackets below) cannot be ruled out since not all specimens were dissected: *Selenia kentaria* (*S. alciphaeria*), *Apamea cogitata* (*Apamea phutonia*), and *Euxoa tessellata*

(*Euxoa messoria*, *E. declarata*). Voucher specimens are deposited in the University of Alberta Strickland Museum.

Statistical analyses

To model the effect of forest fragmentation on alternate host abundance, I used log-linear regressions with Poisson-distributed errors (Agresti 1996). Abundance was modelled separately for each species at three scales of forest fragmentation (200m, 400m, and 600m) using the S-PLUS 2000 statistical software package (MathSoft 1999). To meet the assumptions of the Poisson model, the dispersion parameter Φ (variance : mean) should be close to 1 (Connor *et al.* 1997). If the sampling variance is significantly greater than that predicted by the model (i.e. overdispersed), setting $\Phi = 1$ may result in erroneous conclusions, since the standard errors are underestimated. The Pearson statistic, X^2 , may be used to test for overdispersion (Connors *et al.* 1997):

$$X^2 = \Phi (n - p - 1)$$

where **n** is the number of sampling points and **p** is the number of co-efficients estimated in the model. X^2 follows a Chi-squared distribution, with $(n - p - 1)$ degrees of freedom. The model can be corrected for overdispersion by standardizing observed values of x_i , that is x_i / Φ . Since count data (with a Poisson distribution) is truncated at zero, analysis of abundance changes of rare species (those which were not present at many sites) is not likely to yield meaningful results. Therefore, species with low total counts (arbitrarily set at less than 20) were not subject to loglinear regression.

The response of rare species (those with total abundances lower than 20) to forest fragmentation was quantified using logistic regression on species presence / absence. Species that which were represented by at least one individual at 25% to 75% of the sites were analysed. Since there was some overlap between the criteria used for Poisson and logistic regression (species represented by more than 20 individuals, but present at less than 75% of the sites), I performed logistic regressions only on the >20-group of species which did not show a significant change in abundance.

The species richness of potential parasitoid hosts at each site was calculated using the Margalef Index (Magurran 1988):

$$d = (S - 1) / \ln N$$

where *S* equals the number of species recorded and *N* equals the total number of individuals. This index provides a simple measure of species richness corrected for sample size, and species richness-based indices such as this have a greater discriminatory ability than evenness- or dominance-based indices (Magurran 1988). Data for both years were combined for the 12 sites, which were sampled in 1999 and 2000, while the remaining 12 sites were sampled only in 2000. The effect of forest fragmentation on species diversity was modelled with polynomial regressions using SPLUS 2000 (MathSoft 1999). The response variable (*d*) is distributed normally (Magurran 1988). Models were fitted separately to forest cover data at each of the three spatial scales.

RESULTS

Host assemblages of FTC parasitoids

Most FTC parasitoids are polyphagous or oligophagous, the exceptions being *Leschenaultia exul* and *Aleiodes malacosomatos*, which have to date been reared only from *Malacosoma* species (Table 4.2). The parasitoids that cause the highest mortality of FTC in outbreak and collapsing populations have the narrowest host range. A total of 123 lepidopteran hosts have been reported in the literature for the 17 parasitoids addressed in this study. Of these known hosts, 22 were recorded in this study, and an additional 54 moth species were considered to be potential hosts (Table 4.3) based on the host range criteria listed previously.

The host species of FTC parasitoids are representative of most macrolepidopteran families found in North America, and also occasionally include microlepidopteran species (Table 4.2). However, the number of species in several groups is disproportionately higher than expected at random; the host assemblage is more diverse in the Lasiocampidae, Saturniidae, Sphingidae, Arctiidae, Lymantriidae, Notodontidae and Acronictinae (Noctuidae) when compared to the North American fauna (Fig. 4.2). The families Arctiidae, Saturniidae and Noctuidae contain the highest proportion of FTC parasitoid hosts, each constituting approximately 18% of the host assemblage (Fig. 4.2). I considered the Acronictinae separately from the remainder of the Noctuidae, because they form a unique group within this family: larvae are both arboreal (tree- and shrub-feeding) and have a hairy integument (with the exception of *Simyra henrici*, which is

only sparsely hairy and bores in cattail stems). Very few other noctuids exhibit the combinations of being hairy and arboreal, and the acronictines are more similar to lasiocampids, lymantriids and some notodontids in this respect.

The Geometridae and non-acronictine Noctuidae are under-represented in the assemblage of FTC parasitoid hosts. These host use patterns remain when compared to the known hosts of Nearctic tachinid flies (Arnaud 1978), with the exception of the Acronictinae (Fig. 4.2). The Acronictinae form a higher proportion of the Nearctic tachinid hosts than they do of the FTC parasitoid hosts, and the Nearctic lepidopteran fauna generally. The species richness of both the Nearctic lepidopteran fauna and the tachinid host fauna are dominated by the Geometridae (27.9% and 13.9%, respectively) and the Noctuidae (58.3% and 45.0%) (Figure 4.2).

Host abundance and diversity

A total of 50,877 individual moths representing 335 species were recorded in this study during 1999 and 2000 (see Appendix A and B). Of the total number of species recorded, 76 were either known hosts or considered to be potential hosts of the FTC parasitoids included in this study. FTC moths varied in abundance between years, but remained at undetectable larval densities throughout this study. In 1999, the total number of FTC caught (224) was approximately 4 times higher than the mean number of specimens per species (54). Trap catch in 2000 indicated that FTC abundance was substantially lower than in 1999 (38 individuals compared to total species mean of 96). A summary of the regression results for trap catch as a function of forest fragmentation is presented in Table

4.4 using the spatial scale which best explained the variation in either abundance or probability of occurrence. Of the 53 host species subject to a regression analysis of abundance on forest structure, 40 (75%) showed a significant ($p < 0.05$) response to increasing forest fragmentation in at least one of the sampling years (Table 4.4). An additional four species showed marginally significant ($0.05 < p < 0.10$) responses to forest fragmentation.

Response to forest fragmentation was species-specific, with most species showing a positive or negative response, while a few species showed no obvious response.

Abundance declined significantly with increased forest fragmentation for 40% (21 / 53) of the host species, and an additional seven species were less likely to occur (presence / absence) at sites that were fragmented. Seventeen species showed a positive response to fragmentation (Table 4.4), either through increased abundance (13 species) or higher probability of occurrence (four species). Nine species showed no significant effect of fragmentation in either year. For those regressions that were significant in both years, the direction of the slope (positive or negative) was consistent between years.

Three species, *Apamea commoda* (Wlk.), *Apamea niveivenosa* (Grt.) and *Gluphisia septentrionis* Wlk., showed significant abundance changes in 1999 but not in 2000, despite an increased sample size and higher mean catch in 2000. This pattern may have been due to chance (Type I error, [Zar 1999]). The large difference in trap catch between 1999 and 2000 for *Platartia parthenos* (0 to 653) is due to the fact that this species has a biennial life cycle in Alberta (Schmidt 2000). Increasing the number of sampling sites in

2000 resulted in significant regressions of abundance on fragmentation for most species that showed non-significant results in 1999.

Of the 17 FTC parasitoid species considered here, data on host (both potential and reported) abundance were available for 13 parasitoid species. The host assemblages for 11 of the 13 parasitoid species were predominantly negatively affected by forest fragmentation (Fig. 4.3). Hosts of *Euexorista futilis* generally showed a positive response to fragmentation. Hosts of *Carcelia malacosomae* were distributed equally among those that showed a positive response (2 species) or a negative response (2 species). The one potential alternate host of *Aleiodes malacosomae* considered here (*Phyllodesma americana* [Harr.]) showed no significant change in abundance with fragmentation.

The diversity of host species (d) at the 24 sites ranged from 4.68 to 9.15 (Fig. 4.4), with a mean of 7.16. Host diversity decreases significantly with forest fragmentation at all spatial scales (Table 4.5). A quadratic polynomial model explained variation in site diversity significantly better than did the linear model at the 200m and 400m scale; at 600m, the quadratic term did not significantly improve the model fit over a linear model (Table 4.5). The quadratic model at the 400m scale provided the overall best fit, with fragmentation explaining 55% of the variation in host diversity (Fig. 4.4).

DISCUSSION

Host assemblage of FTC parasitoids - Diptera:

Carcelia malacosomae Sellers - This tachinid fly is common in FTC populations in Alberta, and can cause up to 40% mortality of mature larvae (J. Roland, unpublished data). This species has one generation per year (Williams *et al.* 1996), and the known alternative hosts consist of macrolepidopteran larvae (Table 4.2) that are all either hairy or spiny (with the exception of *Archips argyrospila*). *C. malacosomae* females lay pedicellate (stalked) eggs on the hairs or spines of host larva, so it appears that potential hosts are restricted to this morphology type. The phenological synchrony of *C. malacosomae* with its hosts restricts potential hosts to those that are present in early summer as mature larvae; *Malacosoma*, *Hemileuca maia* and *Archips argyrospila* overwinter as eggs, and are in the larval stage when *Carcelia* adults are active. The arctiids hibernate as partially grown larvae and resume development the following year. *Datana integerrima* hibernates in the pupal stage, so larvae of this species may escape parasitism by *C. malacosomae* in the northern parts of its range where *Datana* is univoltine. In the southern parts of its range, *D. integerrima* has multiple generations, so larvae of the second generation may be available early enough to be vulnerable to *Carcelia*. Based on phenology and larval morphology, the most likely alternative hosts of *C. malacosomae* in central Alberta are species of *Grammia* (Arctiidae) (Table 4.2).

Chaetogaena edwardsii (Williston) - *C. edwardsii* is a common parasitoid of *Malacosoma californicum* that occasionally attacks FTC. This tachinid fly oviposits macrotype eggs on the head capsule or integument of late instar larvae, and is univoltine

(Williams *et al.* 1996). Known hosts cover a broad range of taxonomic groups, including diprionid sawflies (Arnaud 1978) and several unrelated families of Lepidoptera (Table 4.2). Despite the taxonomic diversity of *C. edwardsii* hosts, there are several unifying traits in this host assemblage. With the exception of *Anaea andria* (the larvae of which live in leaf shelters), the hymenopteran and lepidopteran hosts live as exposed defoliators, primarily on broadleaf trees and shrubs. Many of the hosts also feed gregariously, including *Malacosoma*, *Datana ministra*, *Symmerista canicosta*, and *Nymphalis antiopa*. The use of solitary defoliators as hosts may be rare. For example, although *Orgyia leucostigma* has been reported as a host, *C. edwardsii* was not reared from over 20,000 larvae of *Orgyia* collected by the Forest Insect Survey (Raizenne 1952).

The records of *C. edwardsii* from *Euxoa* cutworms (Noctuidae) are unusual. Parasitism of *Euxoa* species by *C. edwardsii* is probably very rare, since *Euxoa* larvae are nocturnal and rest below the soil surface during the day (Lafontaine 1987). This behaviour would protect larvae from tachinids ovipositing directly onto hosts. Since *C. edwardsii* is univoltine, it is restricted to hosts that hibernate as adults and reproduce early in the spring (*Nymphalis antiopa*), and those overwintering as eggs (*Malacosoma*, *Orgyia*). The notodontids reported as hosts overwinter as pupae, and univoltine species hibernating in this stage are in the larval stage in late summer, too late in the season to be susceptible to *C. edwardsii*. However, many Notodontids have multiple yearly broods in the southern parts of their range (Wagner *et al.* 1997), so second generation larvae can be attacked. The only known alternate hosts that occur in central Alberta are sawflies (Hymenoptera),

Nymphalis antiopa, *Malacosoma californicum*, and members of the genus *Orgyia*. The use of *Euxoa* as hosts needs further investigation.

***Euexorista futilis* (Osten Sacken)** - The tachinid fly *Euexorista futilis* is a relatively rare parasitoid of FTC in Alberta (Parry 1995). This species lays micro-type eggs on foliage that is ingested by the host. Two generations a year are produced (Williams *et al.* 1996), so the prevalence of this species in FTC populations is limited by the need for a second host. With the exception of *Malacosoma*, *Ennomos* and *Antheraea polyphemus*, the known hosts of *E. futilis* (Table 4.2) feed on low growing, herbaceous plants and grasses. Unlike *Leschenaultia* and *Patelloa*, which also lay micro-type eggs on foliage, *E. futilis* is apparently a generalist parasitoid of Lepidopteran species that feed primarily on herbs and grasses.

There are no other obvious morphological or behavioural traits that are common to the known hosts of *E. futilis*. For this reason, I have restricted the host assemblage of this parasitoid to species previously reported as hosts, and species congeneric with these hosts.

***Exorista mella* (Walker)** - this tachinid fly has been reared from many species of Lepidoptera (Table 4.2) and several sawfly species (Arnaud 1978). Although it is usually a rare parasitoid of FTC, it can be locally abundant in some outbreaks (Williams *et al.* 1996). Macro-type eggs are deposited directly onto the integument of host larvae, and there are two generations annually. The wide range of lepidopteran host taxa suggest *E.*

mella is a host generalist, in part due to the fact that two different hosts must be used within one season. Although this species oviposits onto the integument of the host, the most suitable hosts appear to be larvae that are spiny or hairy; most of the reported hosts (27 of 42) are densely hairy, and an additional eight species are sparsely hairy or spiny. Only four species (*Danaus plexippus*, *Callosamia promethea*, *Pseudaletia unipuncta*, *Pyreferra hesperidago*) lack hairs or spines. Suitable hosts for *E. mella* in central Alberta should therefore include members of the families Arctiidae, Lasiocampidae, Lymantriidae, Notodontidae (*Nadata*, *Clostera*, *Schizura*), and Noctuidae (Acronictinae).

***Leschenaultia exul* (Townsend)** - *L. exul* is an important tachinid parasitoid of FTC, occasionally causing mortality rates as high as 65% (Parry 1995). This species oviposits micro-type eggs on foliage that is being fed upon by *Malacosoma* larvae (Bess 1936), and there is one generation annually. *L. exul* has only been recorded from *Malacosoma disstria* and *M. americanum*, and is likely a specialist on *Malacosoma*. Ovipositing females of *L. exul* are attracted only to volatiles emitted by trembling aspen and balsam poplar that has sustained feeding damage by FTC (Mondor & Roland 1997). Although *M. americanum* moths oviposit on *Prunus*, later-instar larvae may disperse onto other plants, including *Populus* (Fitzgerald 1995), where they would be exposed to *L. exul* eggs. The absence of *L. exul* records on *M. californicum*, which feeds primarily on rosaceous trees and shrubs (Stehr & Cook 1968), further supports the notion that *L. exul* specializes on the *Malacosoma*-*Populus* system. The close association of the *L. exul* - *Malacosoma* relationship would preclude any significant use of alternative hosts by *L. exul*.

***Lespesia frenchii* (Williston)** - this tachinid often becomes abundant in declining populations of FTC (Parry 1995). Like *C. edwardsii* and *E. mella*, macrotype eggs are deposited onto the integument of the host. This species has at least two annual generations, and is extremely polyphagous. Nearly 60 species of lepidopteran hosts (Table 4.2) have been recorded for *L. frenchii*. Although the known hosts include members from 12 families of Lepidoptera, there are several noteworthy patterns in host use by *L. frenchii*. Most of the known hosts of *L. frenchii* feed exclusively or primarily on trees and shrubs (48 of 58 species). *L. frenchii* also appears to prefer physically large hosts; over half of the hosts (33 / 58) are swallowtails (Papilionidae), sphinx moths (Sphingidae) and giant silk moths (Saturniidae). These three families include the largest species of Lepidoptera in North America. Also noteworthy is the absence of hosts in the family Geometridae (one record of an unidentified species [Table 4.2]). Geometrid moths are the second-most speciose family in North America (Hodges 1983), and are often the dominant tree-feeding species in forested habitats (Wagner *et al.* 1997). The absence of Geometrid host use by the highly polyphagous *L. frenchii* may be a result of the fact that Geometrid larvae exhibit superb cryptic colouration and morphology, and/or that they are of inadequate size for suitable parasitoid development.

L. frenchii may prefer physically large host larvae because they are easier to find (assuming visual cues are important to searching), or because multiple larvae can develop in larger hosts (Belshaw 1994). As such, most conspicuous and large tree- and shrub-feeding Lepidoptera should be suitable hosts for *L. frenchii*.

***Pattelloa pachypyga* (Aldrich & Webber)** - This is an important parasitoid of FTC in outbreak populations, and can cause up to 50% mortality (Roland & Taylor 1995). There is one generation annually, and the microtype eggs of *P. pachypyga* on aspen foliage are ingested by FTC (Williams *et al.* 1996). *P. pachypyga* is thought to be a specialist parasitoid, normally attacking only *M. disstria* (Sippell 1957, Witter & Kulman 1972). Arnaud (1978) lists two other hosts, *Nymphalis antiopa* (Nymphalidae) and *Euproctis chrysorrhea* (Lymantriidae). Larvae of *N. antiopa*, like FTC, feed on aspen and are gregarious in their early instars. *E. chrysorrhea* is an introduced species that primarily feeds on fruit trees, and its range is restricted to the eastern seaboard (Ferguson 1978). *P. pachypyga* females are preferentially attracted to the FTC-aspen complex (as opposed to balsam poplar) suggesting that *P. pachypyga* does not normally search for hosts on trees other than aspen (Mondor & Roland 1997). Support for this specialization is presented by the fact that *P. pachypyga* has never been reared on other species of *Malacosoma*, which feed primarily on rosaceous trees and shrubs (Stehr & Cook 1968).

In a study of the ecology of *Enargia decolor*, a noctuid moth that occasionally causes local defoliation of aspen, Smerenka (1970) reported 'low' levels of *P. pachypyga* parasitism. *E. decolor* and *N. antiopa* have phenologies synchronized with *P. pachypyga* (overwintering as eggs and adults, respectively), further suggesting they could indeed be valid host. Further work on the host range of *P. pachypyga* may show that it is not as specialized on FTC as previously thought.

E. decolor and its congener *E. infumata* were recorded during this study, and I have included these, in addition to *Ipimorpha pleonectusa* (which is closely related and shares a similar niche) in the host range of *P. pachypyga* (Table 4.3).

***Arachnidomyia aldrichi* (Parker) and *Agria housei* Shewell** - These two sarcophagid flies attack FTC in the pupal stage and are two of the most important mortality agents in FTC outbreaks. *A. aldrichi* and *A. housei* can cause up to 90% and 7% pupal mortality, respectively (Parry 1995, J. Roland, unpublished data). Both species are univoltine, and larviposit onto the host pupa or cocoon (Williams *et al.* 1996). A range of taxonomically unrelated hosts are used by these species (Table 4.2), although all hosts are in the pupal stage (overwintering as adults, eggs, or partially grown larvae) earlier in the season than most Lepidoptera (those that overwinter as pupae) when the sarcophagids are reproducing. Only hosts that have exposed pupae, or that pupate above ground in cocoons, are known as hosts. Although *A. aldrichi* is able to kill healthy FTC pupae (Bess 1936), successful parasitism on gypsy moth (*Lymantria dispar*) is dependent on pupae previously killed by ichneumonid wasp attacks (Campbell 1963). The saprophytic nature of Sarcophagids in general (Shewell 1987), and the host use biology of *A. aldrichi* and *A. housei*, suggest these species are only facultative parasitoids of FTC. Many species with a phenology synchronous to that of *A. aldrichi* and *A. housei* and pupating above ground, may be suitable hosts for these species.

Hymenoptera:

***Aleiodes malacosomatos* (Mason)** - The braconid wasp *Aleiodes malacosomatos* is the most important hymenopteran parasitoid of larval FTC, with parasitism rates ranging between 10% and 12% during the early phase of outbreaks (Parry 1995). The only other confirmed hosts of this species are *M. californicum* (subspecies *pluviale* and *lutescens*) and *M. americanum* (Table 4.2). *A. malacosomatos* attacks third instar larvae, and completes development within the same season, emerging from pupae in June (*personal observation*). It is not known if this braconid is multivoltine, although a second generation, following that on *Malacosoma*, is likely given the short, early-season development period of the first generation. Most members of the genus *Aleiodes* are double-brooded in Europe (Shaw 1994), with the second host occupying niches similar to the first generation host. One possible alternate host of *A. malacosomatos* is *Phyllodesma americana* (Harr.), a lasiocampid moth that is sympatric with *Malacosoma* over most of North America. *P. americana* is in the larval stage in June, when first generation *A. malacosomatos* would presumably be searching for hosts. Other species that are sympatric with *M. disstria* over parts of its range, such as the fall webworm (*Hyphantria cunea* [Drury]), may also be suitable hosts.

***Gambrus canadensis canadensis* (Prov.) and *Iseropus stercorator orgyiae* (Ashm.)** - these species occasionally attack FTC, and may have 2 generations per year (Parry 1995). Both species are pupal parasitoids that can have multiple adults emerging from one host pupa. Alternative hosts are few (Table 4.2), but appear to be restricted to species that pupate in trees and shrubs.

***Itoplectis conquisitor* (Say)** - This ichneumonid wasp is one of the most common hymenopteran parasitoids of FTC, and is especially prevalent prior to outbreak population levels (Sippell 1957). *I. conquisitor* is extremely polyphagous, with nearly 70 reported Lepidopteran hosts in 17 families (Table 4.2) in addition to two sawfly (Hymenoptera) genera (Krombein *et al.* 1979). Since this wasp is multivoltine, a large number of hosts are used; *I. conquisitor* can have up to 5 generations annually in southern Ontario (Arthur 1965). In the eastern U.S., *I. conquisitor* overwinters in a host cocoon, and completes one generation in the spring prior to attacking *Malacosoma americanum*. Upon emerging from *Malacosoma* pupae in early July, adults complete an additional two generations before seeking a host in which to overwinter in (Fiske 1903). The life cycle of *I. conquisitor* on FTC is likely very similar to that described by Fiske (1903), although there may only be three or four generations annually in Alberta. Usually a primary parasitoid of pupae, *I. conquisitor* is also occasionally a facultative hyperparasitoid on other ichneumonids and braconids (Krombein *et al.* 1979). The assemblage of known hosts shows that this species prefers to attack small to medium-sized Lepidoptera which spin loose cocoons in trees and shrubs (those species for which this information is available), particularly tree- and shrub-feeding Tortricidae and Pyralidae. Several genera pupate in leaf litter (*Argyrotaenia*, *Rhyacionia* and *Hemileuca*) or shallow underground chambers (*Dryocampa rubicunda*), evidence that *I. conquisitor* females search both vegetation and ground litter for pupae. The absence of cocoon-forming saturniid hosts, such as *Hyalophora*, *Antheraea polyphemus* and *Actias luna* (species for which parasitoids are relatively well documented [Tuskes *et al.* 1996]), may indicate that

cocoons of these species are too tough for *Itoplectis* females to penetrate. Alternatively, the ovipositor may be too short to reach pupae inside double-walled cocoons (for example *Hyalophora* species). It appears that almost any lepidopteran host that pupates above ground is a suitable host for *I. conquisitor*, especially species of Tortricidae and Pyralidae.

***Phobocampe clisiocampae* (Weed)** - *P. clisiocampae* attacks late instar larvae of *Malacosoma*, and is occasionally reared from FTC in Alberta (Williams *et al.* 1996). This ichneumonid wasp may have two generations annually; evidence supporting the occurrence of a second generation is given by hosts that have a later seasonal phenology than *Malacosoma* (Table 4.2). Adults of the Sphingidae, *Actias luna*, and Notodontidae are in the adult stage at about the time *Malacosoma* are larvae, and would provide a cohort of larvae for second-generation *P. clisiocampae*. Alternative hosts of *P. clisiocampe* appear to be restricted to deciduous tree-feeding sphingids and notodontids (with one record from *Actias luna* [Saturniidae]).

***Pimpla pedalis* (Cresson) and *Theronia atalantae* (Cresson)** - These ichneumonids are both polyphagous pupal parasitoids, usually present in low numbers in Alberta populations of FTC (Williams *et al.* 1996). *P. pedalis* has at least two generations annually, so it is dependent on hosts other than FTC. It is unclear if *T. atalantae* has more than one generation in Alberta (Williams *et al.* 1996). A wide variety of hosts are attacked by both species (Table 4.2), but hosts are almost exclusively limited to those which spin cocoons in trees and shrubs; the only hosts which do not exhibit this trait are

four butterfly species, and possibly *Leucania linia* and *Pseudaletia unipuncta* (Noctuidae) (Table 4.2).

***Aprostocetus esurus* (Riley)** - Of the pupal parasitoids attacking FTC, *A. esurus* is the most abundant hymenopteran in Alberta (Parry 1995). *A. esurus* is a polyembryonic eulophid wasp with one generation annually, and has been recorded from a relatively wide variety of Lepidoptera (Table 4.2), representing five families. Host use by this species may be restricted by its small size (adults are less than 3 mm long), so only pupae which are naked or within loosely spun cocoons are vulnerable to attack since this species' short ovipositor precludes oviposition on hosts with thick or tightly spun cocoons.

Forest fragmentation effects on alternate hosts

Forest fragmentation brought on by anthropogenic disturbances has been a central concern for present-day habitat and species diversity losses. A large body of literature on invertebrate responses to habitat fragmentation has accumulated over the last decade, focusing primarily on the patterns of species abundance and diversity. Relatively little is known about subsequent effects on ecosystem processes (Didham *et al.* 1996). Habitat fragmentation effects on invertebrate predator-prey interactions have recent received attention in both agricultural and forested landscapes (e.g. Marino & Landis 1996, Roland & Taylor 1997, Tscharrntke 2000). Landscape structure effects on the parasitoid-host dynamics of the forest tent caterpillar have been relatively well studied; although

many of the FTC parasitoids are polyphagous, the role of alternate hosts in population dynamics and the effects of fragmentation on host assemblages remains unexplored.

To determine how forest structure affects host availability, and ultimately how these patterns may influence the dynamics of the FTC-parasitoid system, I compared and characterized host use patterns of the dominant FTC parasitoids based on literature records, and deduced the most likely alternate hosts in central Alberta. The effect of changing forest structure was assessed on both alternate host abundance and alternate host diversity. Finally, I make several predictions of FTC population dynamics based on parasitoid host range and lepidopteran responses to forest fragmentation.

The host ranges of FTC parasitoids suggest that most species are host generalists (in the phylogenetic sense), capable of attacking species in more than one family (Table 4.2). Caution should be exercised, however, in drawing conclusions about the breadth of host range; host records in the literature may often include spurious records because of species misidentifications, and pest species from which many rearings have been obtained are generally over-represented (Belshaw 1994). Host use may also vary through space (over the geographic range of a parasitoid) and time (at different host densities). With these limitations in mind, however, literature records still provide valuable insight into the ecology of a parasitoid, including relative measures of host range and host ecological characters. In general, the host species of FTC parasitoids are dominated by arboreal (tree- and shrub feeding) Lepidoptera (Fig. 4.2) in the families Sphingidae, Lasiocampidae, Saturniidae, Notodontidae and Lymantriidae. Although most arctiid

caterpillars are herbaceous plant feeders, many of those represented as hosts are arboreal (*Lophocampa* spp., *Halysidota* spp., *Spilosoma virginica*, and *Hyphantria cunea*). The fact that parasitoid hosts share the same feeding niche with the FTC (exposed, arboreal foliage feeders) is not surprising, since polyphagous parasitoids search for hosts with similar ecological characteristics, and are often not restricted by host phylogeny (Sheehan 1994, Shaw 1994). Tachinid flies in general also appear to show a preference for arboreal hosts; Sheehan (1994) found that the arboreal feeding habits of Lepidoptera were a strong predictor of tachinid species richness. Several parasitoid species are notable exceptions to the predominance of arboreal hosts, namely *Carcelia malacosomae* and *Euexorista futilis*. These two tachinid flies appear to prefer hosts encountered on low-growing vegetation. Four of the eight known hosts of *C. malacosomae* are in the Arctiidae, while those of *E. futilis* include a range of herb-feeding noctuids. The alternate hosts of *C. malacosomae* are represented equally by species that increased or decreased in abundance with forest fragmentation. Literature records of *C. malacosomae* hosts suggest species that inhabit open, non-forested habitats (*Grammia*, *Notarctia*) may be important hosts. If this were true, it would be expected that *C. malacosomae* prefers open habitat where a wider range of hosts can be found, and that continuous forest is less suitable habitat. Landscape patterns of *C. malacosomae* parasitism rates on FTC support this view of habitat preference: parasitism rates are higher in fragmented forest stands than in contiguous forest (Roland & Taylor 1997). In contrast, all other dominant tachinids, with narrower host ranges, exhibit decreased parasitism success with fragmentation.

Alternate hosts remain unknown for two species of FTC parasitoids. *Leschenaultia exul*, which can cause up to 30% mortality in FTC in Alberta (Parry 1995), has only been reared from FTC. This tachinid responds to chemical cues emitted through feeding damage of FTC on trembling aspen (Mondor & Roland 1997), and may be a host specialist. Experimental laboratory and field rearing data is needed to provide a better understanding of the true host range of this important FTC parasitoid. *Aleiodes malacosomatos* has only been reared from species of *Malacosoma*; given that adults emerge from third or fourth instar larvae in late June, I believe this species is bivoltine and has an as yet undiscovered alternate host. The host range of this genus has been well studied in Great Britain, and European *Aleiodes*, with phenologies similar to that of *A. malacosomatos* have another generation on hosts which inhabit niches similar to the first generation hosts (Shaw 1983, 1994).

In an agricultural landscape matrix, arboreal lepidopteran hosts of FTC parasitoids are negatively affected by forest fragmentation. Most arboreal species (68%) were either less likely to occur at a site, or showed a significant decline in abundance at sites with lower surrounding forest cover. Herb-feeding species, in contrast, generally showed a positive response (79% of species) to fragmentation, which is not surprising given that herbaceous plant cover is greater in an agricultural (vs. forested) landscape. However, many of these species, such as *Apamea*, *Leucania*, *Mamestra* and *Nephelodes*, which feed primarily on grasses, are reputed hosts for only three FTC parasitoids (*Euexorista futilis*, *Pimpla pedalis*, and *Exorista mella*).

The diversity of the host assemblage showed a marked decline with increasing forest fragmentation at all spatial scales (Table 4.5), although there was some indication that diversity may increase slightly with moderate amounts of fragmentation (Fig. 4.4). Positive effects of natural habitat heterogeneity on diversity could explain this. Natural openings in the forest canopy, such as wetlands, increase the diversity of those species dependent on this habitat. At the 400m scale, diversity declined sharply at sites that were more than 50-60% fragmented. Similarly, Kretschmer & Hoffman (1997) found a linear decrease in bee, carabid beetle and butterfly diversity between 5% and 30% uncultivated lands. In theory, enhanced biodiversity should provide the best means by which ecosystems can adapt to changes in the environment such as habitat fragmentation (LaSalle 1993). Empirical evidence for this is sparse, and the outcomes are not always as predicted. For example, Menalled *et al.* (1999) found that parasitoid diversity and parasitism rates were not necessarily higher in complex landscapes (successional cropland and non-cropland) compared to simple landscapes (cropland). These results may have been influenced by scale-dependent effects (i.e. parasitoids responding to a different scale than that which was measured), or by spatial asynchrony in parasitoid-host dynamics between study sites. Although depauperate parasitoid diversity reflects host diversity (Tscharntke 2000, Kruess & Tscharntke 2000), the effects on parasitism rates and subsequent population dynamics are not necessarily intuitive. Given that forest fragmentation has a negative impact overall on FTC parasitoid host diversity, the diversity of generalist parasitoids, in turn, is likely higher in contiguous forest. Whether this decrease in parasitoid diversity translates into lower FTC parasitism rates remains to

be examined, but this prediction is congruent with long term FTC population dynamics (Roland 1993).

Although the response of host diversity and host abundance to landscape structure is not only specific to the host in question, but also to the parasitoid species, a common pattern emerges from landscape structure effects on host assemblages. Both host abundance and diversity decrease with decreasing forest cover, implying that parasitoids are faced with greater host resource limitations in fragmented landscapes. FTC parasitoids also appear to exhibit lower host search success in fragmented landscapes (Roland & Taylor 1997). When these factors are taken into account, in addition to possible adult nectar source limitations in fragmented landscapes (Kruess & Tscharntke 1994), it is perhaps not surprising that habitat fragmentation has a greater negative impact on parasitoids than on their herbivorous hosts (Kruess & Tscharntke 2000).

Habitat heterogeneity is known to impact FTC population dynamics through a number of factors, such as decreased viral transmission (Roland & Kaupp 1995), and differential parasitoid efficacy (Roland *et al.* 1997). The diminished effect of these mortality agents is associated with greater duration of FTC outbreaks in fragmented forests (Roland 1993). The spatial scale which best explains variation in FTC parasitism is correlated to parasitoid body size, with physically smaller species responding to landscape structure at correspondingly smaller scales (Roland & Taylor 1997). This suggests that dispersal ability (and subsequently search behaviour) is an important determinant of parasitoid success as a function of habitat structure.

In addition to body size, forest structure effects on parasitoid success may be exacerbated by resource availability; parasitoids should be relatively more successful in habitats where their resources (both adult and larval) are greater. In the case of tent caterpillar parasitoids, the host assemblages of most generalists are negatively affected by fragmentation (Fig. 4.3). This suggests that the abundance of generalist FTC parasitoids is variable over space, even though variation in abundance over time may not fluctuate significantly. Conversely, parasitoids with a narrow host range (such as *Leschenaultia exul* and *Patelloa pachypyga*) should show greater variation in abundance through time because they are dependent on the FTC's cyclic populations. Parasitoids with a broader host range have more stable populations (Hassell 1978) because they are able to switch hosts when FTC densities become too low. For this reason, generalist parasitoids should be relatively more important than specialists during the endemic phase of the FTC cycle. Very little data exists on parasitism of FTC at low densities (largely due to the inherent difficulty in finding larvae and cocoons in the field). Preliminary data (J. Roland) shows that, in fact, generalist parasitoids are very important at low FTC densities. The highest parasitoid-caused mortality of pupae is attributable to ichneumonid wasps, primarily *Itopectis conquisitor*, *Theronia atalantae*, and *Gambrus canadensis*. Further evidence for the importance of *I. conquisitor* in endemic FTC populations is presented by the fact that this species causes higher parasitism rates in the early stages of an outbreak (Parry 1995). These ichneumonid species have, as I have shown here, a broader host range than do the tachinid flies prevalent during outbreaks. Because the host assemblages of the Ichneumonidae in this study showed a marked decrease in abundance with forest

fragmentation, I would predict that, overall, ichneumonid wasps have higher rates of FTC parasitism in large, continuous forest stands. This parallels the notion that generalist parasitoids are better suited to searching for hosts in late successional habitats (Price 1994). Incipient outbreaks might therefore exhibit a more rapid rate of increase in fragmented areas, leading to longer outbreak duration (Roland 1993).

Given that the most important parasitoids (those causing the highest mortality rates) of FTC in epidemic populations have a relatively narrow host range, alternate hosts are likely not very important to FTC population dynamics in outbreak and collapsing populations. To add to this, the functional response of parasitoids to high FTC densities, which are several orders of magnitude greater than most Lepidoptera, would preclude the importance of alternate hosts as a significant resource for parasitoids.

Admittedly, the accuracy with which conclusions can be drawn about the effects of changing host resources on the complex population dynamics between parasitoids and multiple hosts is limited to specific knowledge of host use. The spotty and generally poor knowledge of parasitoid biology and taxonomy hinder an in-depth understanding of this system. I have attempted to base my predictions on the most likely host use scenarios, and much remains to be resolved about FTC parasitoids and their hosts. We will likely never know the host range of all the FTC parasitoids, but the Lepidoptera associated with the parasitoid-FTC-aspen system are undoubtedly an integral part of the functioning of this community.

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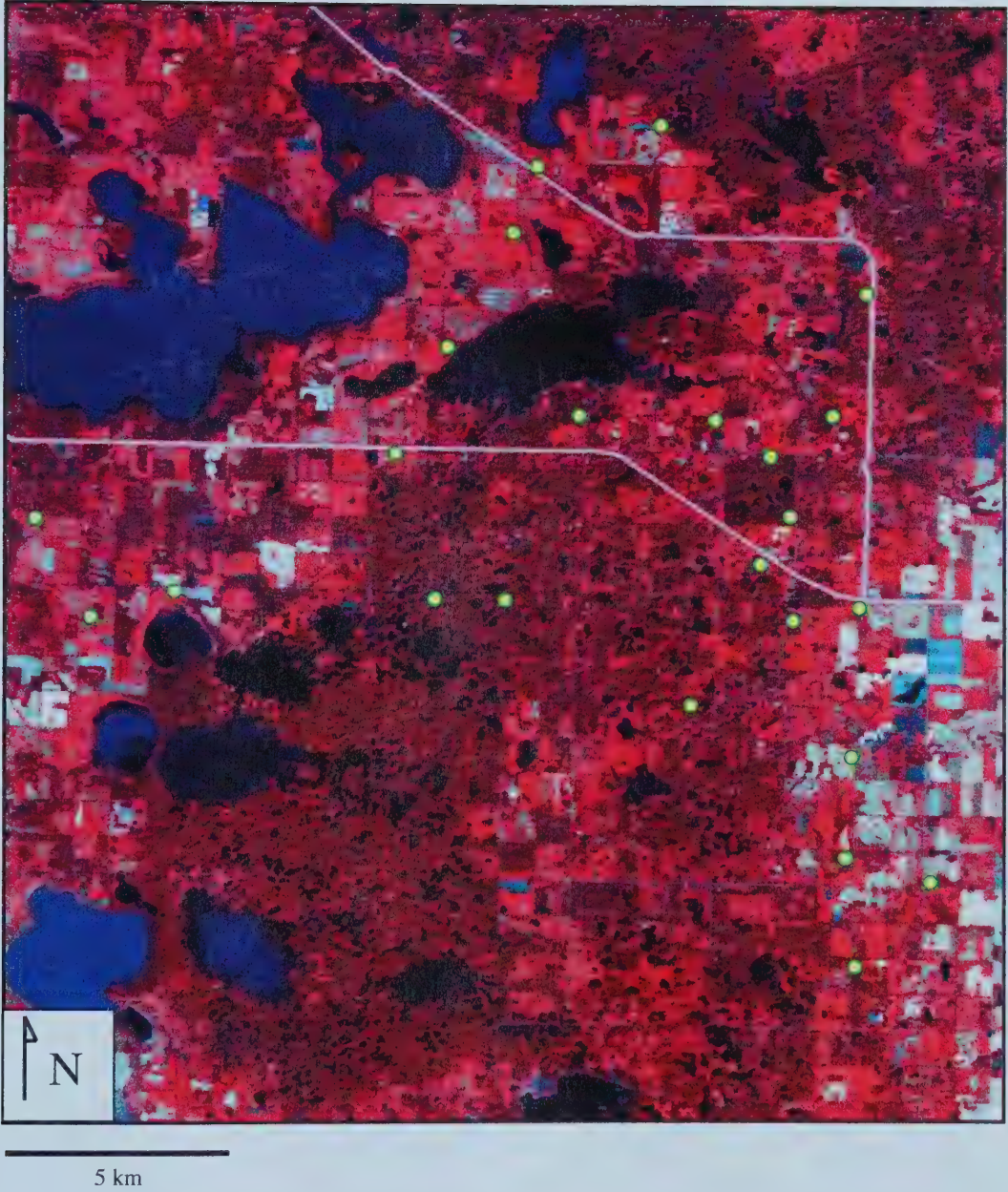


Figure 4.1: Infrared aerial photograph of the Ministik Hills, Alberta. Sampling points are given in yellow. Aspen forests are visible as dark red areas. Secondary highway 630 (top) and Highway 14 (bottom) are indicated in pink.

Table 4.1: Locations and forest fragmentation indices of sites used in this study.

Site	Latitude		Longitude		Fragmentation ¹		
					200m	400m	600m
21.0	53 °	27.12 ' N	112 °	52.59 ' W	31.9	54.0	54.3
27.0	53 °	27.23 ' N	112 °	55.20 ' W	59.7	78.9	85.1
35.5	53 °	26.41 ' N	112 °	55.60 ' W	94.1	90.9	89.0
39.1	53 °	25.68 ' N	112 °	48.27 ' W	41.5	52.0	46.5
43.0	53 °	24.96 ' N	112 °	57.03 ' W	42.3	72.3	82.1
44.0	53 °	24.21 ' N	112 °	54.14 ' W	5.0	26.4	28.6
54.5	53 °	23.73 ' N	112 °	58.95 ' W	76.8	91.9	80.4
59.5	53 °	22.94 ' N	112 °	51.19 ' W	89.8	94.6	77.6
60.0	53 °	23.74 ' N	112 °	50.24 ' W	39.4	45.1	41.6
61.0	53 °	24.05 ' N	112 °	48.47 ' W	53.5	58.7	62.3
63.5	53 °	23.22 ' N	113 °	7.13 ' W	82.9	88.3	80.5
73.0	53 °	22.94 ' N	112 °	49.76 ' W	35.3	37.9	41.4
78.0	53 °	21.58 ' N	114 °	4.32 ' W	69.3	80.6	85.1
79.0	53 °	21.94 ' N	113 °	2.51 ' W	85.8	86.9	76.8
82.0	53 °	22.00 ' N	112 °	57.18 ' W	39.4	26.9	26.6
83.0	53 °	22.00 ' N	112 °	55.83 ' W	41.4	34.2	28.6
85.5	53 °	22.42 ' N	112 °	50.08 ' W	67.7	70.4	65.4
86.0	53 °	21.82 ' N	112 °	49.77 ' W	64.0	53.1	52.4
87.0	53 °	22.03 ' N	112 °	48.31 ' W	80.5	88.8	86.0
98.0	53 °	20.62 ' N	112 °	51.87 ' W	17.1	22.8	30.0
100.5	53 °	20.06 ' N	112 °	48.44 ' W	84.1	88.0	90.2
126.0	53 °	18.72 ' N	112 °	48.44 ' W	70.9	73.6	72.0
127.0	53 °	18.55 ' N	112 °	46.87 ' W	72.7	71.7	73.2
139.0	53 °	17.58 ' N	112 °	48.35 ' W	44.0	52.6	57.4

1 - percent non-forest vs. forest at a radius of 200m, 400m, and 600m.

Table 4.2: Reported lepidopteran hosts of *M. disstria* parasitoids. Parasitoids listed are those reported from Alberta by Parry (1995).

PARASITOID	HOST	FAMILY	Source
Diptera			
Tachinidae			
<i>Carcelia malacosomae</i>			
	<i>Archips argyropila</i> (Wlk.)	Tortricidae	1
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	1
	<i>Hemileuca maia</i> complex	Saturniidae	1
	<i>Datana integerrima</i> G. & R.	Notodontidae	1
	<i>Grammia ornata</i> (Pack.)	Arctiidae	1
	<i>Notarctia proxima</i> (G.-M.)	Arctiidae	1
	<i>Arachnis picta</i> Pack.	Arctiidae	1
	<i>Hypercompe permaculata</i> (Pack.)	Arctiidae	1
<i>Chaetogena edwardsii</i>			
	<i>Anaea andria</i> Scudder	Nymphalidae	1
	<i>Asterocampa celtis</i> (Bsdvl. & LeC.)	Nymphalidae	1
	<i>Nymphalis antiopa</i> (L.)	Nymphalidae	1
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	1
	<i>Datana integerrima</i> G. & R.	Notodontidae	1
	<i>Datana ministra</i> (Drury)	Notodontidae	1
	<i>Symmerista canicosta</i> Franc.	Notodontidae	1
	<i>Orgyia leucostigma</i> (J.E. Sm.)	Lymantriidae	1
	<i>Euxoa messoria</i> (Harr.)	Noctuidae	1
	<i>Euxoa ochrogaster</i> (Gn.)	Noctuidae	1
<i>Euexorista futilis</i>			
	<i>Ostrinia nubilalis</i> (Hbn.)	Pyrilidae	1
	<i>Thymelicus lineola</i> (Ochs.)	Hesperiidae	1
	<i>Nymphalis milberti</i> (Godart)	Nymphalidae	1
	<i>Vanessa atalanta</i> (L.)	Nymphalidae	1
	<i>Vanessa cardui</i> (L.)	Nymphalidae	1
	<i>Ennomos subsignaria</i> (Hbn.)	Geometridae	1
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	1
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	1
	<i>Antheraea polyphemus</i> (Cramer)	Saturniidae	1

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
	<i>Grammia oithona</i> (Strecker)	Arctiidae	1
	<i>Apantes phalerata</i> (Harr.)	Arctiidae	1
	<i>Euchaetias egle</i> (Drury)	Arctiidae	1
	<i>Pyrrharctia isabella</i> (J.E. Sm.)	Arctiidae	1
	<i>Apamea apamiformis</i> (Gn.)	Noctuidae	1
	<i>Autographa californica</i> (Speyer)	Noctuidae	1
	<i>Hyppa xylinoides</i> (Gn.)	Noctuidae	1
	<i>Nephelodes emmedonia</i> (Cramer)	Noctuidae	1
	<i>Nycteola</i> spp.	Noctuidae	1
	<i>Sideridis maryx</i> (Gn.)	Noctuidae	1
<i>Exorista mella</i>			
	<i>Nymphalis antiopa</i> (L.)	Nymphalidae	1
	<i>Polygonia interrogationis</i> (F.)	Nymphalidae	1
	<i>Danaus plexippus</i> (L.)	Danaidae	1
	<i>Phylodesma americana</i> (Harr.)	Lasiocampidae	1
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	1
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	1
	<i>Malacosoma constrictum</i> (H. Edw.)	Lasiocampidae	1
	<i>Malacosoma incurvum</i> (H. Edw.)	Lasiocampidae	1
	<i>Tolyte laricis</i> (Fitch)	Lasiocampidae	1
	<i>Tolyte velleda</i> (Stoll)	Lasiocampidae	1
	<i>Callosamia promethea</i> (Drury)	Saturniidae	1
	<i>Hemileuca oliviae</i> Cockerell	Saturniidae	1
	<i>Datana integerrima</i> G. & R.	Notodontidae	1
	<i>Datana ministra</i> (Drury)	Notodontidae	1
	<i>Clostera inclusa</i> (Hbn.)	Notodontidae	1
	<i>Schizura concinna</i> (J.E. Sm.)	Notodontidae	1
	<i>Grammia nevadensis</i>	Arctiidae	1
	<i>Grammia oithona</i> (Strecker)	Arctiidae	1
	<i>Apantes phyllira</i> (Drury)	Arctiidae	1
	<i>Cynia tenera</i> Hbn.	Arctiidae	1
	<i>Spilosoma virginica</i> (F.)	Arctiidae	1
	<i>Estigmene acraea</i> (Drury)	Arctiidae	1
	<i>Euchaetes egle</i> (Drury)	Arctiidae	1
	<i>Halysidota harrisii</i> Walsh	Arctiidae	1
	<i>Halysidota tessellaris</i> (J.E. Sm.)	Arctiidae	1

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
<i>Hyphantria cunea</i> (Harr.)		Arctiidae	1
<i>Pyrrharctia isabella</i> (J.E. Sm.)		Arctiidae	1
<i>Dasychira basiflava</i> (Pack.)		Lymantriidae	1
<i>Dasychira vagans</i> (B. & McD.)		Lymantriidae	1
<i>Euproctis chrysorrhea</i> (L.)		Lymantriidae	1
<i>Orgyia antiqua</i> (L.)		Lymantriidae	1
<i>Orgyia leucostigma</i> (J.E. Sm.)		Lymantriidae	1
<i>Orgyia pseudotsugata</i> (J.E. Sm.)		Lymantriidae	1
<i>Orgyia vetusta</i> (Bsdvl.)		Lymantriidae	1
<i>Lymantria dispar</i> (L.)		Lymantriidae	1
<i>Leucoma salicis</i> (L.)		Lymantriidae	1
<i>Acronicta americana</i> (Harr.)		Noctuidae	1
<i>Acronicta lepusculina</i> Gn.		Noctuidae	1
<i>Acronicta rubricoma</i> Gn.		Noctuidae	1
<i>Mamestra configurata</i> Wlk.		Noctuidae	16
<i>Pseudaletia unipuncta</i> (Haw.)		Noctuidae	1
<i>Pyreferra hesperidago</i> (Gn.)		Noctuidae	1
<i>Simyra henrici</i> (Grt.)		Noctuidae	1
<i>Leschenaultia exul</i>			
<i>Malacosoma americanum</i> (F.)		Lasiocampidae	1
<i>Malacosoma californicum pluviale</i>		Lasiocampidae	19
<i>Lespesia frenchii</i>			
Unidentified		Pyalidae	1
<i>Pieris rapae</i> (L.)		Pieridae	1
<i>Papilio machaon oregonius</i> Edw.		Papilionidae	1
<i>Papilio eurymedon</i> Lucas		Papilionidae	1
<i>Papilio canadensis</i> Rothschild & Jordan		Papilionidae	1
<i>Papilio glaucus</i> L.		Papilionidae	1
<i>Papilio multicaudata</i> Kirby		Papilionidae	1
<i>Papilio polyxenes</i> F.		Papilionidae	1
<i>Papilio rutulus</i> Lucas		Papilionidae	1
<i>Papilio troilus</i> L.		Papilionidae	1
<i>Nymphalis antiopa</i> (L.)		Nymphalidae	1
<i>Vanessa cardui</i> (L.)		Nymphalidae	1
Unidentified		Geometridae	1

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
<i>Malacosoma americanum</i> (F.)		Lasiocampidae	1
<i>Malacosoma californicum</i> (Pack.)		Lasiocampidae	1
<i>Malacosoma constrictum</i> (H. Edw.)		Lasiocampidae	1
<i>Anisota rubicunda</i> (F.)		Saturniidae	1
<i>Anisota senatoria</i> J.E. Sm.		Saturniidae	1
<i>Anisota virginiensis</i> (Drury)		Saturniidae	1
<i>Citheronia regalis</i> (F.)		Saturniidae	1
<i>Eacles imperialis</i> (Drury)		Saturniidae	1
<i>Actias luna</i> (L.)		Saturniidae	1
<i>Antheraea polyphemus</i> (Cramer)		Saturniidae	1
<i>Automeris io</i> (F.)		Saturniidae	1
<i>Callosamia promethea</i> (Drury)		Saturniidae	1
<i>Eupackardia calleta</i> (West.)		Saturniidae	1
<i>Hyalophora columbia</i> Smith		Saturniidae	1
<i>Hyalophora cecropia</i> (L.)		Saturniidae	1
<i>Hyalophora euryalus</i> (Bsdvl.)		Saturniidae	1
<i>Samia cynthia</i>		Saturniidae	1
<i>Syssphinx bicolor</i> (Harr.)		Saturniidae	1
<i>Ceratomia amyntor</i> (Hbn.)		Sphingidae	1
<i>Ceratomia catalpae</i> (Bsdvl.)		Sphingidae	1
<i>Ceratomia undulosa</i> (Wlk.)		Sphingidae	1
<i>Manduca quinquemaculata</i> (Haw.)		Sphingidae	1
<i>Pachysphinx modesta</i> (Harr.)		Sphingidae	1
<i>Paonias myops</i> (J.E. Sm.)		Sphingidae	1
<i>Smerinthus cerysii</i> Kirby		Sphingidae	1
<i>Smerinthus jamaicensis</i> (Drury)		Sphingidae	1
<i>Sphinx chersis</i> (Hbn.)		Sphingidae	1
<i>Sphinx kalmiae</i> (J.E. Smith)		Sphingidae	1
<i>Datana angusii</i> G. & R.		Notodontidae	1
<i>Datana integerrima</i> G. & R.		Notodontidae	1
<i>Datana ministra</i> (Drury)		Notodontidae	1
<i>Clostera inclusa</i> (Hbn.)		Notodontidae	1
<i>Spilosoma virginica</i> (F.)		Arctiidae	1
<i>Euchaetes egle</i> (Drury)		Arctiidae	1
<i>Halisidota caryae</i> (Harr.)		Arctiidae	1
<i>Hyphantria cunea</i> (Harr.)		Arctiidae	1
<i>Orgyia leucostigma</i> (J.E. Sm.)		Lymantriidae	1
<i>Euproctis chrysorrhea</i> (L.)		Lymantriidae	1
<i>Lymantria dispar</i> (L.)		Lymantriidae	1
<i>Leucoma salicis</i> (L.)		Lymantriidae	1

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
	<i>Faronta diffusa</i> (Wlk.)	Noctuidae	1
	<i>Heliothis zea</i> (Boddie)	Noctuidae	1
	<i>Hydraecia immanis</i> Gn.	Noctuidae	1
	<i>Hypsoropha hormos</i> Hbn.	Noctuidae	1
<i>Patelloa pachypyga</i>			
	<i>Nymphalis antiopa</i> (L.)	Nymphalidae	1
	<i>Euproctis chrysorrhea</i> (L.)	Lymantriidae	1
	<i>Enargia decolor</i> (Wlk.)	Noctuidae	12
Sarcophagidae			
<i>Agria housei</i>			
	<i>Acleris variana</i> (Fern.)	Tortricidae	11
	<i>Choristoneura conflictana</i> (Wlk.)	Tortricidae	11
	<i>Choristoneura fumiferana</i> (Clem.)	Tortricidae	11
	<i>Neophasia menapia</i> (F. & F.)	Pieridae	11
	<i>Nymphalis antiopa</i> (L.)	Nymphalidae	11
	<i>Nepytia canosaria</i> (Wlk.)	Geometridae	11
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	11
	<i>Orgyia pseudotsugata</i> (J.E. Sm.)	Lymantriidae	11
	<i>Leucoma salicis</i> (L.)	Lymantriidae	11
<i>Arachnidomyia aldrichi</i>			
	<i>Choristoneura pinus</i> (Free.)	Tortricidae	8
	<i>Choristoneura fumiferana</i> (Clem.)	Tortricidae	13
	<i>Dioryctria abietivorella</i>	Pyalidae	6
	<i>Anisota rubicunda</i>	Saturniidae	13
	<i>Lymantria dispar</i> (L.)	Lymantriidae	4
	<i>Leucoma salicis</i> (L.)	Lymantriidae	5
Braconidae			
<i>Aleiodes malacosomatos</i>			
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	14
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	14

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
<hr/>			
Ichneumonidae			
<i>Gambrus canadensis</i>			
<i>Archips cerasivorana</i> (Fitch)		Tortricidae	7
<i>Cydia pomonella</i> (L.)		Tortricidae	7
<i>Thymelicus lineola</i> (Ochs.)		Hesperiidae	7
<i>Malacosoma americanum</i> (F.)		Lasiocampidae	7
<i>Malacosoma californicum</i> (Pack.)		Lasiocampidae	7
<i>Orgyia leucostigma</i> (J.E. Sm.)		Lymantriidae	2
<i>Iseropus stercorator orgyiae</i>			
<i>Choristoneura rosaceana</i> (Harr.)		Tortricidae	7
<i>Ctenucha virginica</i> (Esper)		Arctiidae	7
<i>Halysidota</i> sp.		Arctiidae	7
<i>Orgyia leucostigma</i> (J.E. Sm.)		Lymantriidae	7
<i>Orgyia vetusta</i> (Bdv.)		Lymantriidae	7
<i>Simyra henrici</i> (Grt.)		Noctuidae	7
<i>Itoplectis conquisitor</i>			
<i>Hyaloscotes pithopoera</i> (Dyar)		Psychidae	7
<i>Oiketicus abbotii</i> Grt.		Psychidae	7
<i>Thyridopteryx ephemeriformis</i> (Haw.)		Psychidae	7
<i>Coleophora pruniella</i> Clem.		Coleophoridae	7
<i>Coleophora trifolli</i> (Curt.)		Coleophoridae	7
<i>Epermia cicutaella</i> Kft.		Eperminiidae	7
<i>Anacampsis inocuella</i> (Zell.)		Gelechiidae	7
<i>Dichomeris marginella</i> (F.)		Gelechiidae	7
<i>Acleris hastiana</i> (L.)		Tortricidae	7
<i>Acleris minuta</i> (Rob.)		Tortricidae	7
<i>Ancylis comptana</i> (Froel.)		Tortricidae	7
<i>Aphelia alleniana</i> (Fern.)		Tortricidae	7
<i>Archips argyrospila</i> (Wlk.)		Tortricidae	7
<i>Archips cerasivorana</i> (Fitch)		Tortricidae	7
<i>Archips georgiana</i> (Wlk.)		Tortricidae	7
<i>Archips rileyana</i> (Grt.)		Tortricidae	7
<i>Argyrotaenia cockerellana</i> (Kft.)		Tortricidae	7

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
	<i>Argyrotaenia pinatubana</i> (Kft.)	Tortricidae	7
	<i>Argyrotaenia velutinana</i> (Wlk.)	Tortricidae	7
	<i>Choristoneura conflictana</i> (Wlk.)	Tortricidae	7
	<i>Choristoneura fumiferana</i> (Clem.)	Tortricidae	7
	<i>Choristoneura lambertiana</i> (Bsk.)	Tortricidae	7
	<i>Choristoneura pinus</i> (Free.)	Tortricidae	7
	<i>Choristoneura rosaceana</i> (Harr.)	Tortricidae	10
	<i>Cnephasia interjectana</i> (Haw.)	Tortricidae	7
	<i>Evora hemidesma</i> (Zell.)	Tortricidae	7
	<i>Paralobesia viteana</i> (Clem.)	Tortricidae	7
	<i>Rhyacionia buoliana</i> (D. & S.)	Tortricidae	7
	<i>Rhyacionia bushnelli</i> (Bsk.)	Tortricidae	7
	<i>Rhyacionia frustrana</i> (Com.)	Tortricidae	7
	<i>Sparganothis flavibasana</i> (Fern.)	Tortricidae	7
	<i>Sparganothis pettitana</i> (Rob.)	Tortricidae	7
	<i>Spilonota ocellana</i> (D. & S.)	Tortricidae	7
	<i>Xenotemna pallorana</i> Rob.	Tortricidae	7
	<i>Geina periscelidactyla</i> (Fitch)	Pterophoridae	7
	<i>Acrobasis betullela</i> Hulst	Pyalidae	7
	<i>Acrobasis rubrifasciella</i> Pack.	Pyalidae	7
	<i>Acrobasis caryvoriella</i> Rag.	Pyalidae	7
	<i>Acrobasis juglandis</i> (LeB.)	Pyalidae	7
	<i>Acrobasis kearfotella</i> Dyar	Pyalidae	7
	<i>Dioryctria reniculella</i> (Grt.)	Pyalidae	7
	<i>Diaphania hyalinata</i> (L.)	Pyalidae	7
	<i>Ostrinia nubilalis</i> (Hbn.)	Pyalidae	7
	<i>Urbanus proteus</i> (L.)	Hesperiidae	7
	<i>Thymelicus lineola</i> (Ochs.)	Hesperiidae	7
	<i>Pieris rapae</i> (L.)	Pieridae	7
	<i>Graphium marcellus</i> (Cramer)	Papilionidae	7
	<i>Cingilia caternaria</i> (Drury)	Geometridae	7
	<i>Lambdina fervidaria</i> (Hbn.)	Geometridae	7
	<i>Lambdina fiscellaria</i> (Gn.)	Geometridae	7
	<i>Ennomos subsignaria</i> (Hbn.)	Geometridae	7
	<i>Nematocampa resistaria</i> (H.-S.)	Geometridae	7
	<i>Rheumaptera hastata</i> (L.)	Geometridae	7
	<i>Thera juniperata</i> (L.)	Geometridae	10
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	7
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	7
	<i>Hemileuca</i> sp.	Saturniidae	7

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
<i>Hemileuca lucina</i>	H. Edw.	Saturniidae	17
<i>Hemileuca oliviae</i>	Ckll.	Saturniidae	17
<i>Callosamia securifera</i>	(Maassen)	Saturniidae	18
<i>Dryocampa rubicunda</i>	(F.)	Saturniidae	7
<i>Cisseps fulvicollis</i>		Arctiidae	15
<i>Hyphantria cunea</i>	(Harr.)	Arctiidae	7
<i>Lymantria dispar</i>	(L.)	Lymantriidae	7
<i>Orgyia antiqua</i>	(L.)	Lymantriidae	7
<i>Orgyia leucostigma</i>	(J.E. Sm.)	Lymantriidae	7
<i>Alabama argillacea</i>	(Hbn.)	Noctuidae	7
<i>Anomis erosa</i>	Hbn.	Noctuidae	7
<i>Exyra semicrocea</i>	(Gn.)	Noctuidae	7
<i>Lascoreia ambigualis</i>	Wlk.	Noctuidae	7
<i>Morissonia confusa</i>	(Hbn.)	Noctuidae	2
<i>Simyra henrici</i>	(Grt.)	Noctuidae	7
<i>Trichoplusia ni</i>	(Hbn.)	Noctuidae	7
<i>Phobocampe clisiocampe</i>			
<i>Malacosoma americanum</i>	(F.)	Lasiocampidae	7
<i>Malacosoma californicum</i>	(Pack.)	Lasiocampidae	7
<i>Actias luna</i>	(L.)	Saturniidae	7
<i>Paonias</i>	sp.	Sphingidae	7
<i>Sphinx</i>	sp.	Sphingidae	7
<i>Datana ministra</i>	(Drury)	Notodontidae	7
<i>Datana perspicua</i>	(G. & R.)	Notodontidae	7
<i>Heterocampa</i>	sp.	Notodontidae	7
<i>Schizura concinna</i>	(J.E. Sm.)	Notodontidae	7
<i>Schizura ipomeae</i>	(Dbldy.)	Notodontidae	7
<i>Schizura semirufescens</i>	(Wlk.)	Notodontidae	7
<i>Schizura unicornis</i>	(J.E. Sm.)	Notodontidae	7
<i>Symmerista canicosta</i>	Franch.	Notodontidae	7
<i>Pimpla pedalis</i>			
<i>Archips argyrospila</i>	(Wlk.)	Tortricidae	7
<i>Argyrotaenia mariana</i>	(Fern.)	Tortricidae	7
<i>Pseudosciaphila duplex</i>	(Walsh)	Tortricidae	7
<i>Epargyrus clarus</i>	(Cramer)	Hesperiidae	7
<i>Neophasia menapia</i>	(F. & F.)	Pieridae	7

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
	<i>Lambdina fiscellaria</i> (Gn.)	Geometridae	7
	<i>Protoboarmia porcelaria</i> (Gn.)	Geometridae	7
	<i>Malacosoma americanum</i> (F.)	Lasiocampidae	7
	<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	7
	<i>Heterocampa guttivitta</i> (Wlk.)	Notodontidae	7
	<i>Ctenucha virginica</i> (Esper)	Arctiidae	7
	<i>Pyrrharctia isabella</i> (J.E. Sm.)	Arctiidae	7
	<i>Halisidota caryae</i> (Harr.)	Arctiidae	7
	<i>Lophocampa maculata</i> (Harr.)	Arctiidae	7
	<i>Dasychira plagiata</i> (Wlk.)	Lymantriidae	7
	<i>Euproctis chrysorrhea</i> (L.)	Lymantriidae	7
	<i>Leucoma salicis</i> (L.)	Lymantriidae	7
	<i>Lymantria dispar</i> (L.)	Lymantriidae	7
	<i>Orgyia antiqua</i> (L.)	Lymantriidae	7
	<i>Orgyia leucostigma</i> (J.E. Sm.)	Lymantriidae	7
	<i>Acronicta americana</i> (Harr.)	Noctuidae	7
	<i>Acronicta</i> sp.	Noctuidae	7
	<i>Leucania linia</i> Gn.	Noctuidae	7
	<i>Pseudaletia unipuncta</i> (Haw.)	Noctuidae	7

Theronia atalantae fulvescens

<i>Choristoneura fumiferana</i> (Clem.)	Tortricidae	7
<i>Neophasia menapia</i> (F. & F.)	Pieridae	7
<i>Nymphalis californica</i> (Bdv.)	Nymphalidae	7
<i>Oreta rosea</i> (Wlk.)	Drepanidae	7
<i>Ennomos subsignaria</i> (Hbn.)	Geometridae	7
<i>Lambdina fiscellaria</i> (Gn.)	Geometridae	7
<i>Nepytia phantasmaria</i> (Stkr.)	Geometridae	7
<i>Malacosoma americanum</i> (F.)	Lasiocampidae	3
<i>Malacosoma californicum</i> (Pack.)	Lasiocampidae	7
<i>Callosamia promethea</i> (Drury)	Saturniidae	7
<i>Hyalophora cecropia</i> (L.)	Saturniidae	7
<i>Dasychira plagiata</i> (Wlk.)	Lymantriidae	7
<i>Euproctis chrysorrhea</i> (L.)	Lymantriidae	7
<i>Leucoma salicis</i> (L.)	Lymantriidae	7
<i>Lymantria dispar</i> (L.)	Lymantriidae	7
<i>Orgyia leucostigma</i> (J.E. Sm.)	Lymantriidae	7
<i>Orgyia pseudotsugata</i> (J.E. Sm.)	Lymantriidae	7

Table 4.2 (continued).

PARASITOID	HOST	FAMILY	source
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Eulophidae			
<i>Aprostocetus esurus</i>			
	<i>Acrobasis juglandis</i> (LeB.)	Pyrilidae	9
	<i>Diatraea saccharalis</i> (F.)	Pyrilidae	9
	<i>Grapholita molesta</i> (Bsk.)	Tortricidae	9
	<i>Gretchena bolliana</i> (Slingerland)	Tortricidae	9
	<i>Choristoneura fumiferana</i> (Clem.)	Tortricidae	9
	<i>Choristoneura pinus</i> (Free.)	Tortricidae	9
	<i>Hyphantria cunea</i> (Harr.)	Arctiidae	9
	<i>Orgyia leucostigma</i> (J.E. Sm.)	Lymantriidae	9
	<i>Euproctis chrysorrhoea</i> (L.)	Lymantriidae	9
	<i>Lymantria dispar</i> (L.)	Lymantriidae	9
	<i>Alabama argillacea</i> (Hbn.)	Noctuidae	9
	<i>Anomis erosa</i> Hbn.	Noctuidae	9

1 - Arnaud (1978), 2 - Butler (1993), 3 - Collins & Weast (1961), 4 - Eggen (1988), 5 - Glendenning (1914), 6 - J. Lill, pers. comm., 7 - Krombein et al. 1979, 8 - Nealis (1991), 9 - Peck (1963), 10 - Raizenne (1952), 11 - Shewell (1971), 12 - Smerenka (1970), 13 - Forest Insect and Disease Suevey, unpubl. data, Sault St. Marie, Ontario, 14 - Stehr & Cook 1968, 15 - Pavuk & Stinner (1991), 16 - O'Hara (1999), 17 - Muesebeck et al. (1951), 18 - Peigler (1985), 19 - Sippell (1957).

Table 4.3 (continued).

HOST

PARASITOID

Species	Family	<i>C. malacosomae</i>	<i>E. futilis</i>	<i>E. mella</i>	<i>L. frenchii</i>	<i>P. pachypyga</i>	<i>A. housei</i>	<i>A. aldrichi</i>	<i>A. malacosomatos</i>	<i>G. c. canadensis</i>	<i>I. stercorator</i>	<i>I. conquisitor</i>	<i>P. clisiocampae</i>	<i>P. pedalis</i>	<i>T. atalantae</i>	TOTAL
<i>Apamea alia</i>	Nc		0													1
<i>Apamea amputatrix</i>	Nc		0													1
<i>Apamea cogitata</i>	Nc		0													1
<i>Apamea commoda</i>	Nc		0													1
<i>Apamea devastator</i>	Nc		0													1
<i>Apamea inficita</i>	Nc		0													1
<i>Apamea lignicolora</i>	Nc		0													1
<i>Apamea niveivenosa</i>	Nc		0													1
<i>Apamea nr. lateritia</i>	Nc		0													1
<i>Apamea sordens</i>	Nc		0													1
<i>Enargia decolor</i>	Nc					X										1
<i>Enargia infumata</i>	Nc					0										1
<i>Ipimorpha pleonectusa</i>	Nc					0										1
<i>Leucania commoides</i>	Nc													0		1
<i>Leucania insueta</i>	Nc													0		1
<i>Leucania multilinea</i>	Nc													0		1
<i>Mamestra configurata</i>	Nc			X												1
<i>Nephelodes minians</i>	Nc		X													1
<i>Pseudaletia unipuncta</i>	Nc													X		1
<i>Simyra henrici</i>	Nc			X							X	X				3
<i>Clostera albosigma</i>	Nt			0	0								0			3
<i>Clostera apicalis</i>	Nt			0	0								0			3
<i>Clostera strigosa</i>	Nt			0	0								0			3
<i>Furcula modesta</i>	Nt				0								0			2
<i>Furcula occidentalis</i>	Nt				0								0			2
<i>Furcula scolopendrina</i>	Nt				0								0			2
<i>Gluphisia septentrionis</i>	Nt				0								0			2
<i>Nadata gibbosa</i>	Nt				0								0			2
<i>Notodonta scitipennis</i>	Nt				0								0			2
<i>Notodonta simplaria</i>	Nt				0								0			2
<i>Odontosia elegans</i>	Nt				0								0			2
<i>Oligocentria semirufescens</i>	Nt				0								X			2
<i>Pheosia rimosa</i>	Nt				0								0			2
<i>Schizura leptinoides</i>	Nt				0								0			2
<i>Schizura unicornis</i>	Nt				0								X			2

Table 4.3 (continued).

HOST		PARASITOID														
Species	Family	1														
		<i>C. malacosomae</i>	<i>E. futilis</i>	<i>E. mella</i>	<i>L. frenchii</i>	<i>P. pachypyga</i>	<i>A. housei</i>	<i>A. aldrichi</i>	<i>A. malacosomatos</i>	<i>G. c. canadensis</i>	<i>I. stercorator</i>	<i>I. conquisitor</i>	<i>P. clisiocampae</i>	<i>P. pedalis</i>	<i>T. atalantae</i>	TOTAL
<i>Antheraea polyphemus</i>	Sa		X		o											2
<i>Paonias excaecatus</i>	Sp				o								X			2
<i>Smerinthus cerisyi</i>	Sp				X								o			2
<i>Smerinthus jamaicensis</i>	Sp				X								X			2
<i>Sphinx vashti</i>	Sp				o								o			2

1: Ar = Arctiidae, Dr = Drepanidae, Ge = Geometridae, La = Lasiocampidae, Ly = Lymantriidae, Nc = Noctuidae, Nt = Notodontidae, Sa = Saturniidae, Sp = Sphingidae.

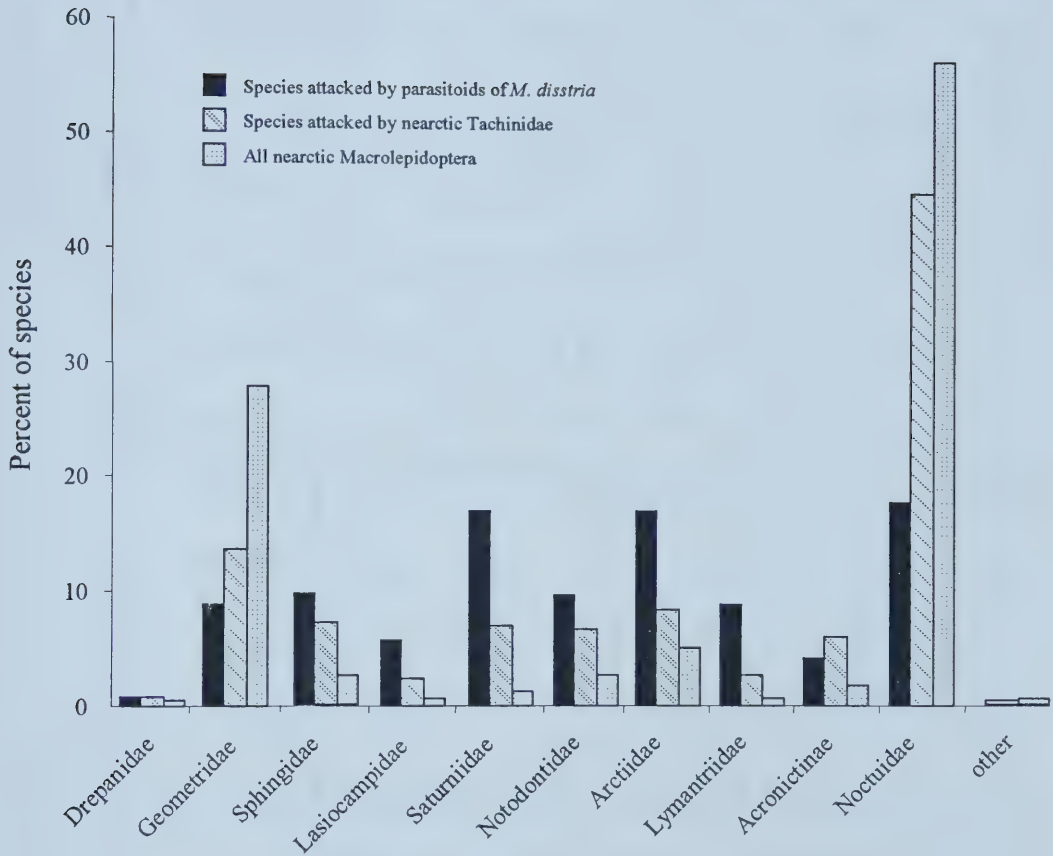


Figure 4.2: Systematic comparison of macrolepidopteran host use by parasitoids of *M. disstria* ($n = 123$ hosts) and nearctic Tachinidae ($n = 416$ hosts) in relation to the North American Macrolepidoptera fauna ($n = 4999$ species). Acronictine and non-acronictine noctuids are shown separately.

Table 4.4 (continued).

Species	Family	Parasitoids	1999						2000						slope			
			Total catch	p value	Model	Intercept	Slope	Dev. expl.	Scale (m)	Total catch	p value	Model	Intercept	Slope	Dev. expl.	Scale (m)	1999	2000
<i>Acronicta radcliffei</i>	Nc	2	3	0.087	Log	1.53	-0.066	0.22	200	0	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	-	---
<i>Apamea amputatrix</i>	Nc	1	6	0.071	Log	-3.30	0.055	0.20	600	6	N.S.	Log	---	---	---	---	+	N.S.
<i>Apamea cogitata</i>	Nc	1	507	<0.001	Pois	-0.48	0.043	0.85	400	1606	<0.001	Pois	-0.48	0.025	0.47	400	+	+
<i>Apamea commoda</i>	Nc	1	123	<0.001	Pois	-1.27	0.040	0.54	200	308	N.S.	Pois	---	---	---	---	+	N.S.
<i>Apamea devastator</i>	Nc	1	35	0.043	Log	-3.00	0.097	0.30	600	198	<0.001	Pois	-3.15	0.051	0.57	600	+	+
<i>Apamea inficita</i>	Nc	1	47	<0.001	Pois	-2.68	0.063	0.66	200	136	0.006	Pois	-0.54	0.020	0.23	600	+	+
<i>Apamea niveivenosa</i>	Nc	1	6	0.023	Log	-5.68	0.090	0.34	400	14	N.S.	Log	---	---	---	---	+	N.S.
<i>Apamea sordens</i>	Nc	1	14	N.S.	Log	---	---	---	---	23	0.029	Pois	-5.52	0.057	0.24	600	---	+
<i>Enargia decolor</i>	Nc	1	61	N.S.	Pois	---	---	---	---	144	N.S.	Pois	---	---	---	---	N.S.	N.S.
<i>Enargia infumata</i>	Nc	1	19	N.S.	Pois	---	---	---	---	15	0.016	Log	1.898	-0.053	---	200	N.S.	-
<i>Ipimorpha pleonectusa</i>	Nc	1	66	<0.001	Pois	0.88	0.025	0.60	200	60	N.S.	Pois	---	---	---	---	+	N.S.
<i>Leucania commoides</i>	Nc	1	37	<0.001	Pois	-2.11	0.056	0.64	200	69	0.026	Pois	-0.80	0.018	0.16	200	+	+
<i>Leucania insueta</i>	Nc	1	45	<0.001	Pois	-4.00	0.076	0.64	200	49	0.072	Log	-1.768	0.034	0.10	200	+	+
<i>Leucania multilinea</i>	Nc	1	99	0.011	Pois	-0.79	0.029	0.41	200	74	0.049	Pois	-1.13	0.019	0.15	600	+	+
<i>Mamestra configurata</i>	Nc	1	6	0.097	Log	-3.82	0.064	0.18	200	0	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	+	---
<i>Nephelodes minians</i>	Nc	1	85	<0.001	Pois	-0.56	0.033	0.53	200	90	0.009	Pois	-1.73	0.026	0.24	200	+	+
<i>Clostera albosigma</i>	Nt	3	155	N.S.	Pois	---	---	---	---	354	0.004	Pois	2.29	-0.010	0.26	200	N.S.	-
<i>Clostera apicalis</i>	Nt	3	36	N.S.	Pois	---	---	---	---	178	N.S.	Pois	---	---	---	---	N.S.	N.S.
<i>Furcula occidentalis</i>	Nt	2	22	N.S.	Pois	---	---	---	---	32	0.047	Pois	1.00	-0.015	0.14	200	N.S.	-
<i>Furcula scolopendrina</i>	Nt	2	35	N.S.	Pois	---	---	---	---	72	N.S.	Pois	---	---	---	---	N.S.	N.S.
<i>Gluphista septentrionis</i>	Nt	2	72	0.026	Pois	-0.05	0.021	0.34	200	240	N.S.	Pois	---	---	---	---	+	N.S.

Table 4.4 (continued).

Species	Family		1999										2000										slope	
	1	2	Total catch	p value	Model	Intercept	Slope	Dev. expl.	4	5	Total catch	p value	Model	Intercept	Slope	Dev. expl.	4	5	1999	2000				
<i>Nadata gibbosa</i>	Nt	2	41	N.S.	Pois	---	---	---	---	---	56	0.038	Pois	1.44	-0.013	0.15	400	400	N.S.	-				
<i>Oligocentria semirufescens</i>	Nt	2	20	N.S.	Pois	---	---	---	---	---	4	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.S.	---				
<i>Pheosia rimosa</i>	Nt	2	72	N.S.	Pois	---	---	---	---	---	240	N.S.	Pois	---	---	---	---	---	N.S.	N.S.				
<i>Schizura leptinoides</i>	Nt	2	11	0.007	Log	6.74	-0.132	0.44	200	200	34	0.043	Pois	0.44	-0.027	0.21	200	200	---	-				
<i>Schizura unicornis</i>	Nt	2	66	N.S.	Pois	---	---	---	---	---	100	0.027	Pois	1.52	-0.014	0.18	400	400	N.S.	-				
<i>Antheraea polyphemus</i>	Sa	2	21	N.S.	Pois	---	---	---	---	---	95	0.013	Pois	2.21	-0.010	0.22	400	400	N.S.	-				
<i>Paonias excaecatus</i>	Sp	2	30	N.S.	Pois	---	---	---	---	---	20	0.020	Pois	1.06	-0.019	0.15	200	200	N.S.	-				
<i>Smerinthus cerisyi</i>	Sp	2	190	N.S.	Pois	---	---	---	---	---	626	N.S.	Pois	---	---	---	---	---	N.S.	N.S.				
<i>Smerinthus jamaicensis</i>	Sp	2	267	N.S.	Pois	---	---	---	---	---	259	0.022	Pois	1.69	-0.011	0.17	200	200	N.S.	-				

1 - abbreviations as those used in Table 4.3. 2 - Number of parasitoids reported or thought to use this host. 3 - Regression model used in analysis. Pois = Poisson regression on total trap catch, Log = logistic regression on presence/absence of species. 4 - Proportion of the deviance explained by the model, i.e. [(Null Dev. - Residual Dev.) / Null Dev]. 5 - Spatial scale at which the model provided the best fit the data.

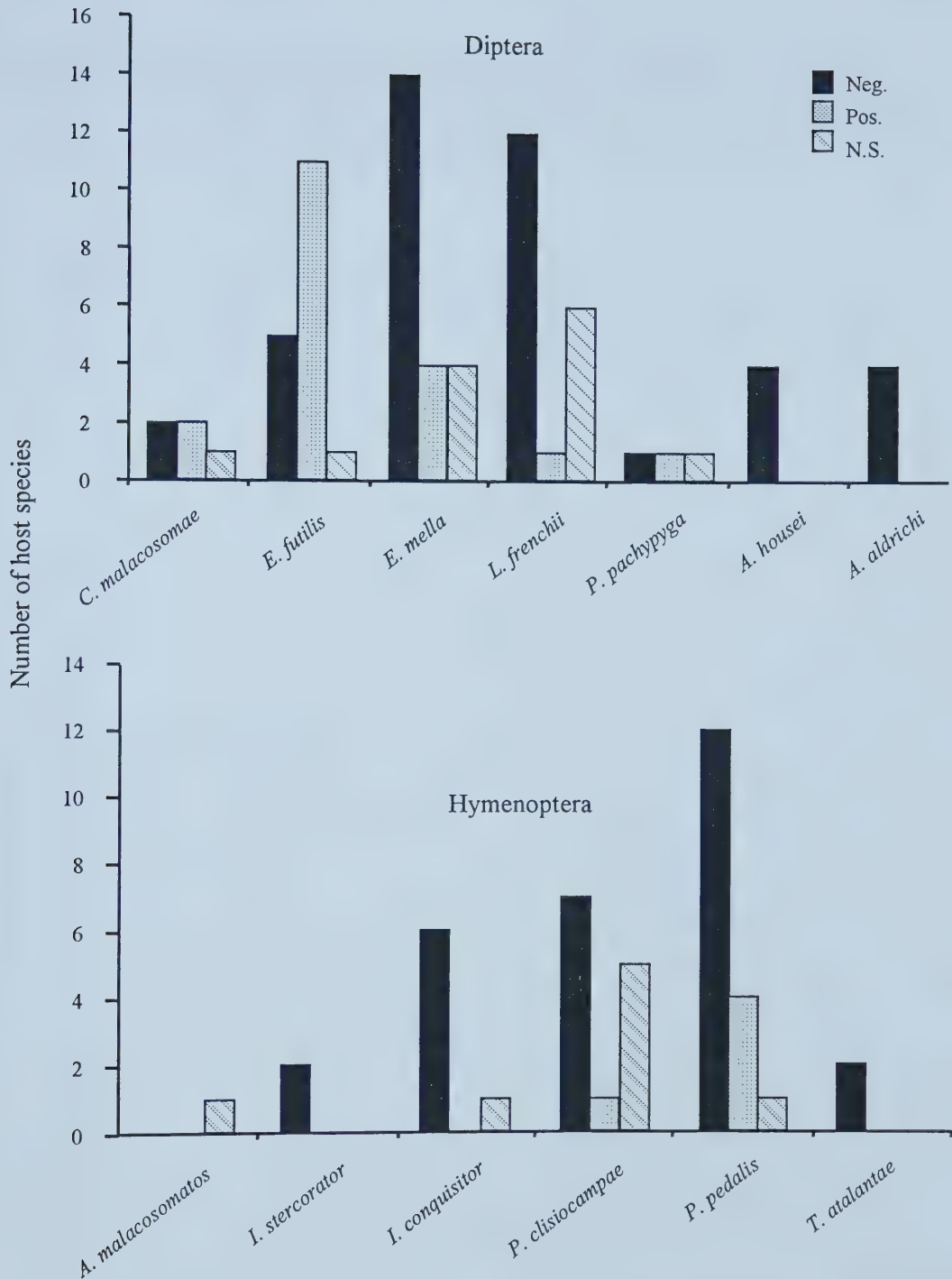


Figure 4.3: Response of alternative host abundance to forest fragmentation at Ministik Hills, Alberta. Data is summarized from regression results in Table 4.4. “Neg.” = decrease in abundance with fragmentation, “Pos.” = increase, “N.S.” = no significant change.

Table 4.5: Regression results of parasitoid host diversity (Margalef Index) as a function forest fragmentation, measured at three spatial scales. A quadratic model ($Y = aX + bX^2 + c$) provided a significantly better fit than a linear model ($Y = aX + c$) at the 200m and 400m scales, but not at the 600m scale.

Scale (m)	<i>p</i> – value	R ²	<i>a</i>	<i>b</i>	<i>c</i>
200	0.002	0.45	0.052	-0.0007	6.94
400	<0.001	0.55	0.082	-0.0009	6.21
600	0.005	0.30	-0.028	-----	8.92

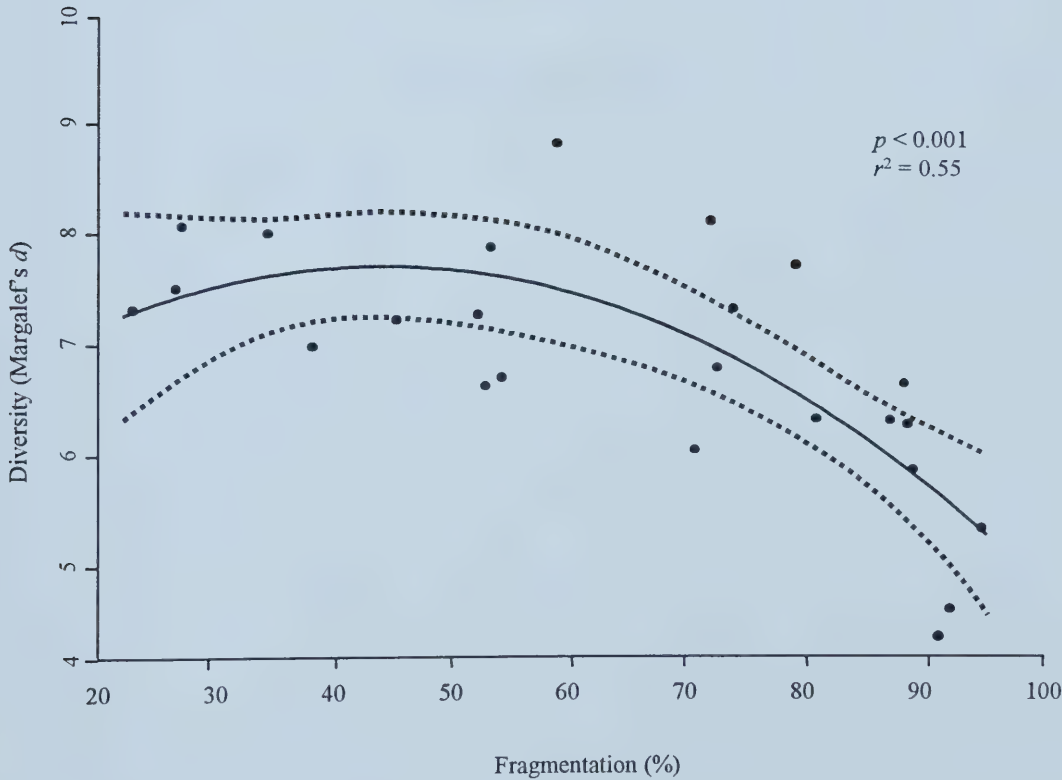


Figure 4.4: Diversity of *M. disstria* alternate hosts as a function of forest fragmentation. Fragmentation is given as percent non-forest at a 400m radius. Dotted line indicates 95% confidence interval.

Chapter 5

GENERAL CONCLUSIONS

A thorough understanding of the population dynamics of any insect depends in large part on our understanding of the ecology of that species during all intervals of its population cycle. Although the forest tent caterpillar is one of several well-studied periodic insect pests, our knowledge of its ecology when populations are at endemic levels is poor. The goals of this thesis were to fill in some of these gaps in our knowledge of endemic FTC population ecology, and to facilitate further research in this field. I approached these objectives by evaluating and improving population monitoring methods using pheromone traps, and by determining the importance of landscape-mediated parasitoid host availability when the FTC as a parasitoid resource becomes limiting, i.e. at endemic FTC population levels.

Population monitoring protocol

To effectively monitor FTC populations through the use of synthetic pheromones, a trapping system should be operational over the range of population variation. To evaluate the performance of synthetic pheromone varieties with respect to population variation, three pheromone blends were field-tested. These blends consisted of 1) the primary constituent only ([5Z,7E] 5,7 dodecadienal), 2) a binary blend (100:1 [5Z,7E] 5,7 dodecadienal : [5Z,7Z] 5,7 dodecadienal), and 3) a tertiary blend (100:1:10 [5Z,7E] 5,7 dodecadienal : [5Z,7Z] 5,7 dodecadienal : Z,7 dodecanal). Trap catches with the tertiary blend relative to the other blends suggest that this pheromone provides a superior lure for capturing FTC adults. The tertiary blend consistently had the highest and most precise trap catch, differentiating more FTC density categories than did either the primary or secondary blend (Chapter 2).

In Chapter 2, I show that pheromone trap catch of FTC moths is dose-dependent.

Polyurethane lures dosed with 8 μ g or less of the binary blend failed to capture FTC moths in endemic populations, while 67 μ g to 390 μ g doses consistently capture moths over the range of FTC population levels tested. Lures dosed at 390 μ g gave the highest mean trap catch, and the lowest rate of zero-captures. Similarly, traps baited with 110 μ g of the tertiary blend were able to resolve FTC abundance in endemic populations, whereas 1 μ g and 11 μ g lures failed to capture moths. Further field trials are needed to determine the dose response of the tertiary blend at lure concentrations greater than those tested here.

Trap efficacy is improved using a polyurethane lure (Flex Lure, Phero Tech Inc., Delta, BC) over traps using red rubber septa (Chapter 3). This appears to be due to the fact that attractiveness of Flex Lures remains constant over at least the first 28d in the field (Chapter 3), whereas rubber septa attractiveness decreases more rapidly (Datterman 1982). The longevity of Flex Lures is sufficient to provide a constant source of pheromone emission over the FTC flight period, given that traps are deployed one to two weeks prior to the onset of adult emergence (Chapter3).

The Universal Moth Trap (Uni-trap) design is superior to that of Sticky Wing Traps for capturing FTC moths, at both endemic and epidemic population levels (Chapter 3). When FTC are scarce, the Uni-trap has higher catch rates, possibly because moths are less likely to escape from these than from sticky-type traps (Sanders 1986), and / or more

individuals are attracted to the Uni-trap because of differing pheromone plume characteristics among trap types (Lewis & Macauley 1976). When FTC moths are abundant, Wing Traps become functionally saturated with moths and are therefore unsuitable for accurate population monitoring.

Parasitoid hosts and forest structure

With the exception of a few species, parasitoids of the forest tent caterpillar prey on other lepidopteran species, both facultatively (alternative hosts) and / or by obligation (alternate hosts). In Chapter 4, I suggest that the lepidopteran hosts are particularly important to generalist parasitoids when FTC levels are very low, at a point in the FTC population cycle when specialist parasitoids are a relatively unimportant mortality source (J. Roland, unpublished data). Spatially structured environments, such as forests fragmented by human disturbance, can significantly alter insect communities (Didham *et al.* 1996) and population dynamics (Marino & Landis 1996, Roland & Taylor 1997, Tscharntke 2000). To attempt a better understanding of the link between forest fragmentation effects on FTC population dynamics and parasitoid host communities, I examined the effect of changing forest cover on both alternate host abundance and alternate host diversity.

Most FTC parasitoids are host generalists, capable of attacking species in more than one family (Chapter 4). In aspen-dominated forests fragmented by agricultural activities, many of these hosts are negatively affected by decreasing forest cover. Most arboreal Lepidoptera species (68%) showed a significant decline in abundance, or were less likely to occur at sites with lower surrounding forest cover. Most herb-feeding species (79%)

showed the opposite trend in abundance or presence / absence with fragmentation.

However, herb-feeding species do not comprise a large part of the parasitoid assemblage, and are therefore not likely to play an important role in FTC-parasitoid dynamics.

Species of *Macrolepidoptera* that are known or potential alternate hosts for FTC parasitoids showed a marked decline in diversity with increasing forest fragmentation.

The strongest effect of forest structure occurred at a spatial scale of 400 meters (i.e. a 400 meter radius), with a sharp decline in diversity at sites that were more than 50-60% fragmented. Similarly, Kretschmer & Hoffman (1997) found a linear decrease in bee, carabid beetle and butterfly diversity between 70% and 95% cultivated lands.

Given that forest fragmentation has an overall negative impact on FTC parasitoid host diversity and abundance, the diversity of generalist parasitoids, in turn, is likely greater in contiguous forest. Although an increase in parasitoid diversity doesn't necessarily result in greater parasitism rates (Menalled *et al.* 1999), greater FTC parasitism and parasitoid diversity in contiguous forest is consistent with long term FTC population dynamics (Roland 1993).

Further research

In addition to the research guidelines suggested in Chapter 3, further studies should address how closely parasitoid community changes reflect changes in the host community, and whether these changes result in spatially structured parasitism rates of endemic FTC populations. With the development of a population monitoring protocol

sensitive to changes in non-outbreak FTC populations, it is now possible to survey the parasitoid fauna of FTC with consecutive, detailed population-density data; knowledge of the parasitoid community during all population stages would provide a better understanding of the importance of alternate hosts, and factors influencing alternate host community composition such as landscape structure. Field and lab research is also needed to confirm many of the hosts reported for FTC parasitoids.

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APPENDIX A. Summary of 1999 trap catch by site.

Family	Species	Checklist # ¹	1999												TOTAL
			27	43	44	60	61	73	82	83	86	98	126	127	
Drepanidae	<i>Habrosyne scripta</i>	6235.0	1	3	1	1	0	2	2	0	3	2	0	1	16
Drepanidae	<i>Pseudothyatra cymatophoroides</i>	6237.0	0	1	2	0	1	2	11	5	1	3	1	0	27
Drepanidae	<i>Euthyatira pudens</i>	6240.0	0	1	2	2	0	5	2	0	0	1	0	0	13
Drepanidae	<i>Drepana arcuata</i>	6251.0	0	0	0	0	1	1	4	0	0	0	0	0	6
Drepanidae	<i>Drepana bilineata</i>	6252.0	0	0	1	0	0	1	0	1	0	1	0	0	4
Drepanidae	<i>Eudelinea herminiata</i>	6253.0	0	2	1	0	1	0	0	0	0	1	3	0	8
Drepanidae	<i>Oreta rosea</i>	6255.0	1	7	2	3	2	1	4	3	0	2	1	0	26
Geometridae	<i>Protitame virginalis</i>	6270.0	0	0	3	1	5	1	0	1	0	11	0	1	23
Geometridae	<i>Iridopsis larvata</i>	6588.0	0	3	1	0	0	3	1	0	1	0	1	1	11
Geometridae	<i>Ectropis crepuscularia</i>	6597.0	0	0	1	0	1	1	0	0	0	0	0	0	3
Geometridae	<i>Protoboarmia porcellaria</i>	6598.0	0	1	4	1	5	2	1	1	2	8	1	0	26
Geometridae	<i>Biston betularia</i>	6640.0	0	0	1	1	0	0	1	2	0	0	2	4	11
Geometridae	<i>Erannis tilitaria</i>	6665.0	0	4	1	0	3	13	3	9	2	8	1	2	46
Geometridae	<i>Cabera erythemaria</i>	6677.0	1	1	4	1	2	3	0	0	0	13	3	3	31
Geometridae	<i>Cabera variolaria</i>	6678.0	0	1	3	0	0	0	0	0	0	0	2	0	6
Geometridae	<i>Euchlaena obtusaria</i>	6726.0	21	21	17	13	23	13	21	13	15	15	13	6	191
Geometridae	<i>Euchlaena johnsonaria</i>	6729.0	1	0	5	1	4	6	2	1	1	0	1	0	22
Geometridae	<i>Euchlaena marginaria</i>	6734.0	0	0	1	1	1	1	0	0	0	1	0	0	4
Geometridae	<i>Euchlaena tigrinaria</i>	6737.0	7	8	13	12	11	26	11	8	15	21	29	13	174
Geometridae	<i>Xanthotype urticaria</i>	6740.0	4	2	1	1	6	8	0	1	1	1	8	3	36
Geometridae	<i>Xanthotype sospeta</i>	6743.0	10	34	43	21	40	45	32	26	22	40	33	2	348
Geometridae	<i>Pero morisonaria</i>	6755.0	6	2	8	7	9	17	36	20	5	15	2	8	135
Geometridae	<i>Campaea perlata</i>	6796.0	19	4	9	4	10	12	1	6	4	16	8	7	100
Geometridae	<i>Ennomos magnaria</i>	6797.0	0	0	1	0	0	0	1	1	1	5	0	1	10
Geometridae	<i>Selenia kenaria</i>	6818.0	0	0	0	2	1	0	1	0	0	1	0	3	8
Geometridae	<i>Metanema inatomaria</i>	6819.0	4	10	14	0	11	4	7	4	4	8	5	4	75
Geometridae	<i>Metanema determinata</i>	6820.0	6	0	5	2	7	1	4	4	1	7	0	3	40
Geometridae	<i>Metarranthis duaria</i>	6822.0	7	17	13	4	9	12	3	5	8	37	9	8	132

Family	Species	Checklist #	1999											TOTAL	
			Site												
			27	43	44	60	61	73	82	83	86	98	126	127	
Geometridae	<i>Anagoga occiduaris</i>	6836.0	3	3	3	1	9	3	4	2	0	9	7	3	47
Geometridae	<i>Proble amicaris</i>	6838.0	3	17	21	11	13	27	6	5	8	28	18	14	171
Geometridae	<i>Plagodis phlogosaria</i>	6842.0	3	3	5	2	6	3	3	1	0	5	3	3	37
Geometridae	<i>Lambdina fuscilaria</i>	6888.0	0	0	0	0	0	1	0	0	0	0	0	0	1
Geometridae	<i>Sycia macularia</i>	6912.0	2	1	0	5	0	1	7	7	1	0	3	5	32
Geometridae	<i>Synaxis jubararia</i>	6954.0	0	1	1	1	0	1	0	0	0	2	0	0	6
Geometridae	<i>Tetraxis crocallata</i>	6963.0	1	3	4	4	5	8	2	3	1	8	4	2	45
Geometridae	<i>Prochoerodes transversata</i>	6982.0	0	2	4	3	3	6	10	2	7	7	4	5	53
Geometridae	<i>Nematocampa resistaria</i>	7009.0	2	14	5	1	12	24	6	6	13	10	16	3	112
Geometridae	<i>Nemoria unitaria</i>	7018.0	3	4	6	10	8	5	3	5	2	8	3	4	61
Geometridae	<i>Synchlora aerata</i>	7058.0	5	2	4	4	4	1	6	3	4	1	2	4	40
Geometridae	<i>Cyclophora pendulinaria</i>	7139.0	1	0	3	1	3	1	0	0	0	1	0	1	11
Geometridae	<i>Scopula inductata</i>	7169.0	0	7	34	0	14	4	0	0	1	5	13	3	81
Geometridae	<i>Mesoleuca ruficollata</i>	7307.0	0	0	1	0	2	0	3	0	0	1	2	0	9
Geometridae	<i>Spargania luctuata</i>	7313.0	26	1	4	0	11	1	5	2	1	3	1	0	55
Geometridae	<i>Anticlea vasilata</i>	7329.0	1	5	2	1	3	1	1	0	1	3	4	1	23
Geometridae	<i>Anticlea multiferrata</i>	7330.0	0	0	0	0	0	0	2	0	0	1	0	0	3
Geometridae	<i>Xanthorhoe lacustrata</i>	7390.0	0	2	2	0	2	4	3	1	0	6	2	1	23
Geometridae	<i>Euphyia unangulata</i>	7399.0	8	6	16	4	5	7	13	1	7	25	16	8	116
Geometridae	<i>Operophtera bruceata</i>	7437.0	0	1	2	0	2	8	0	0	1	4	20	0	38
Geometridae	<i>Eubaphe mendica</i>	7440.0	3	19	16	6	14	8	8	7	15	12	17	25	150
Geometridae	<i>Horisme intestinata</i>	7445.0	10	7	14	6	1	9	5	0	2	8	14	2	78
Geometridae	<i>Eupithecia stellata</i>	7564.0	0	1	0	0	1	0	0	0	1	0	0	0	3
Geometridae	<i>Eupithecia ravocostaliata</i>	7605.0	0	0	0	0	0	0	0	0	0	2	0	1	3
Geometridae	<i>Cladara atrolittrata</i>	7639.0	0	0	0	0	0	0	1	0	0	1	0	1	3
Uranidae	<i>Callizites amorata</i>	7650.0	5	60	27	7	27	12	7	3	4	7	32	5	196
Lasiocampidae	<i>Phylodesma americana</i>	7687.0	4	4	1	0	2	3	3	0	1	2	0	5	25
Lasiocampidae	<i>Malacosoma distria</i>	7698.0	3	3	38	16	1	14	32	19	12	66	10	10	224
Saturniidae	<i>Antheraea polyphemus</i>	7757.0	3	0	4	1	3	1	1	0	5	2	0	1	21
Sphingidae	<i>Smerinthus jamaicensis</i>	7821.0	32	15	24	17	31	30	3	8	9	61	16	21	267
Sphingidae	<i>Smerinthus cerisyi</i>	7822.0	11	19	11	11	14	22	11	20	16	13	17	25	190
Sphingidae	<i>Poonias excaecatus</i>	7824.0	2	3	4	1	4	3	3	2	2	2	3	1	30

Family	Species	Checklist #	1999												TOTAL
			Site												
			27	43	44	60	61	73	82	83	86	98	126	127	
Notodontidae	<i>Clostera albosigma</i>	7895.0	4	22	11	8	20	3	6	5	18	24	15	19	155
Notodontidae	<i>Clostera apicalis</i>	7901.0	5	1	6	0	2	4	1	3	2	4	7	1	36
Notodontidae	<i>Nadata gibbosa</i>	7915.0	2	3	7	1	3	1	4	3	1	6	5	5	41
Notodontidae	<i>Pheosia rimosa</i>	7922.0	4	1	1	1	5	12	6	17	1	12	4	8	72
Notodontidae	<i>Odontostia elegans</i>	7924.0	0	0	0	0	0	0	0	0	1	1	0	0	2
Notodontidae	<i>Notodonta scitipennis</i>	7926.0	0	0	0	0	0	0	0	0	0	0	1	0	1
Notodontidae	<i>Notodonta simplaria</i>	7928.0	0	0	0	0	0	0	1	0	0	0	0	1	2
Notodontidae	<i>Gluphisia septentrionis</i>	7931.0	17	2	4	1	3	5	5	5	8	4	6	12	72
Notodontidae	<i>Furcula occidentalis</i>	7939.0	1	0	4	1	4	1	0	0	1	7	1	2	22
Notodontidae	<i>Furcula scolopendrina</i>	7940.0	2	0	9	2	2	3	1	2	5	2	4	3	35
Notodontidae	<i>Furcula modesta</i>	7941.0	0	2	0	0	1	0	4	0	0	1	1	1	10
Notodontidae	<i>Schizura unicornis</i>	8007.0	5	9	6	6	3	1	6	12	5	10	2	1	66
Notodontidae	<i>Schizura leptinoides</i>	8011.0	0	1	2	1	1	0	1	3	0	2	0	0	11
Notodontidae	<i>Oligocentria semirufescens</i>	8012.0	2	0	1	0	1	2	3	0	3	5	1	2	20
Arctidae	<i>Eilema bicolor</i>	8043.0	0	2	0	0	1	0	1	0	0	0	0	2	6
Arctidae	<i>Clemensia albata</i>	8098.0	29	95	33	5	16	17	21	27	9	31	4	15	302
Arctidae	<i>Haploa lecontei</i>	8111.0	2	0	2	2	1	0	1	0	1	2	1	2	14
Arctidae	<i>Holomeina ferruginosa</i>	8123.0	2	1	0	4	1	4	17	4	0	3	0	2	38
Arctidae	<i>Pyrrharctia isabella</i>	8129.0	0	0	0	0	0	0	0	0	1	0	1	2	4
Arctidae	<i>Esigmene acraea</i>	8131.0	0	0	0	0	0	0	0	0	0	0	0	1	1
Arctidae	<i>Spilosoma congrua</i>	8134.0	0	0	0	0	0	0	0	0	2	0	0	0	2
Arctidae	<i>Spilosoma dubia</i>	8136.0	0	0	1	0	0	0	0	0	0	0	0	0	1
Arctidae	<i>Spilosoma virginica</i>	8137.0	9	6	19	5	2	4	2	4	5	15	6	5	82
Arctidae	<i>Phragmatobia assimilians</i>	8158.0	1	28	7	0	5	8	4	6	7	12	2	3	83
Arctidae	<i>Arctia carya</i>	8166.0	1	0	1	0	1	0	0	2	0	0	1	3	9
Arctidae	<i>Grammia parthenice</i>	8196.0	4	5	0	2	4	2	1	5	3	0	5	5	36
Arctidae	<i>Grammia virgo</i>	8197.0	13	3	12	1	2	5	0	6	10	4	6	2	64
Arctidae	<i>Lophocampa maculata</i>	8214.0	0	0	7	4	20	3	6	3	1	14	2	6	66
Arctidae	<i>Ctenucha virginica</i>	8262.0	24	19	45	5	11	18	27	25	3	26	3	2	208
Arctidae	<i>Cisseps fulvicollis</i>	8267.0	6	4	4	0	2	2	6	23	2	3	0	3	55
Lymantiridae	<i>Dayehira vagans</i>	8294.0	1	0	1	1	2	0	3	3	1	1	0	1	14
Lymantiridae	<i>Orgyia antiqua</i>	8308.0	0	0	1	0	0	0	0	0	0	0	1	0	2

Family	Species	Checklist #	1999													TOTAL
			Site													
			27	43	44	60	61	73	82	83	86	98	126	127		
Lymantriidae	<i>Leucoma salicis</i>	8319.0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Noctuidae	<i>Idia americalis</i>	8322.0	22	17	12	7	19	11	36	17	5	12	6	8	172	
Noctuidae	<i>Idia aemula</i>	8323.0	1	2	0	2	3	1	1	0	0	0	0	1	11	
Noctuidae	<i>Idia nr. aemula</i>	8323.1	0	20	0	1	1	2	0	1	1	0	0	0	26	
Noctuidae	<i>Phalaenophana pyramusalis</i>	8338.0	1	0	1	0	0	2	8	0	2	2	1	2	19	
Noctuidae	<i>Zanclognatha lutealba</i>	8354.0	34	18	24	21	28	27	35	31	44	19	21	17	319	
Noctuidae	<i>Chytolita petrealis</i>	8356.0	13	11	24	13	9	20	8	17	26	12	13	12	178	
Noctuidae	<i>Macrochilo bivittata</i>	8359.0	0	0	2	0	0	0	0	0	0	0	0	0	2	
Noctuidae	<i>Macrochilo louisiana</i>	8361.0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Noctuidae	<i>Phalaenostola metonalis</i>	8362.0	14	23	20	9	36	18	10	11	23	9	25	11	209	
Noctuidae	<i>Phalaenostola hanhami</i>	8365.0	0	3	0	2	0	4	0	2	5	0	2	2	20	
Noctuidae	<i>Palthis angulalis</i>	8397.0	5	1	10	3	10	15	5	3	4	12	10	6	84	
Noctuidae	<i>Rivula propinqualis</i>	8404.0	49	87	54	23	33	29	22	41	37	55	39	21	490	
Noctuidae	<i>Mycterophora inexplicata</i>	8413.0	0	1	0	1	1	0	1	0	1	2	0	1	8	
Noctuidae	<i>Hypena palparia</i>	8444.0	0	0	0	0	1	0	1	0	0	0	0	0	2	
Noctuidae	<i>Hypena atomaria</i>	8450.0	1	9	5	1	9	2	2	1	3	0	2	1	36	
Noctuidae	<i>Hypena edictalis</i>	8452.0	1	28	4	0	8	2	9	8	24	15	53	27	179	
Noctuidae	<i>Lomanaltes eductalis</i>	8455.0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Noctuidae	<i>Scoliopteryx libatrix</i>	8555.0	1	1	0	0	0	1	0	0	0	1	1	0	5	
Noctuidae	<i>Zale minerea</i>	8697.0	0	0	1	0	0	0	1	0	1	2	0	0	5	
Noctuidae	<i>Euclidia cuspidata</i>	8731.0	0	0	0	0	0	1	0	0	0	0	0	0	1	
Noctuidae	<i>Caenurgina crassiuscula</i>	8738.0	2	2	0	1	1	3	0	0	5	0	0	1	15	
Noctuidae	<i>Catocala relicta</i>	8803.0	0	0	0	0	0	0	2	0	0	0	0	1	3	
Noctuidae	<i>Catocala unijuga</i>	8805.0	0	0	0	1	0	0	2	7	0	0	0	0	10	
Noctuidae	<i>Catocala briseis</i>	8817.0	0	0	1	0	0	0	0	3	0	0	0	0	4	
Noctuidae	<i>Catocala semirelicta</i>	8821.0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Noctuidae	<i>Catocala blandula</i>	8867.0	0	0	0	0	0	0	1	0	1	0	0	0	2	
Noctuidae	<i>Abrostola urentis</i>	8881.0	0	7	1	2	3	0	5	0	3	3	6	2	32	
Noctuidae	<i>Diachrysia aeneoides</i>	8896.0	19	14	3	3	7	8	64	15	18	10	31	28	220	
Noctuidae	<i>Diachrysia ballula</i>	8897.0	0	2	0	1	0	0	0	0	0	0	1	0	4	
Noctuidae	<i>Eosphropteryx thyatyroides</i>	8905.0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Noctuidae	<i>Autographa rubida</i>	8909.0	1	1	4	1	1	3	4	2	1	5	2	2	27	

Family	Species	Checklist #	1999													TOTAL
			Site													
			27	43	44	60	61	73	82	83	86	98	126	127		
Noctuidae	<i>Autographa bimaculata</i>	8911.0	1	1	0	1	1	0	1	0	0	0	0	0	0	5
Noctuidae	<i>Autographa mappa</i>	8912.0	1	0	0	0	0	0	0	2	0	0	0	0	0	3
Noctuidae	<i>Autographa pseudogamma</i>	8913.0	0	0	0	0	0	0	0	0	1	0	0	1	2	
Noctuidae	<i>Autographa flagellum</i>	8916.0	0	0	0	0	0	0	0	0	1	0	0	0	1	
Noctuidae	<i>Autographa ampla</i>	8923.0	0	0	0	0	0	0	3	0	0	1	0	0	4	
Noctuidae	<i>Anagrapha falceifera</i>	8924.0	1	0	0	0	0	0	0	0	1	0	0	1	3	
Noctuidae	<i>Syngrapha octoscripta</i>	8926.0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Noctuidae	<i>Plusia putnami</i>	8950.0	9	0	0	1	4	0	1	2	0	0	3	8	28	
Noctuidae	<i>Plusia venusta</i>	8953.0	9	1	2	3	0	3	3	11	3	1	7	3	46	
Noctuidae	<i>Baileya ophthalmica</i>	8970.0	0	0	1	3	2	0	0	1	0	0	0	0	7	
Noctuidae	<i>Nola cilioides</i>	8990.0	0	0	0	0	0	0	0	1	0	1	0	0	2	
Noctuidae	<i>Pseudeva purpurigera</i>	8999.0	1	0	1	0	2	7	1	0	1	3	3	2	21	
Noctuidae	<i>Lithacodia albidula</i>	9048.0	125	62	111	81	82	113	24	43	128	81	40	42	932	
Noctuidae	<i>Lithacodia carneola</i>	9053.0	5	6	2	0	2	1	1	1	2	0	1	7	28	
Noctuidae	<i>Raphia frater</i>	9193.0	26	15	63	6	38	26	15	19	35	53	13	39	348	
Noctuidae	<i>Acrionicta dactylina</i>	9203.0	3	0	0	0	1	1	0	0	0	0	0	0	5	
Noctuidae	<i>Acrionicta lepusculina</i>	9205.0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Noctuidae	<i>Acrionicta innotata</i>	9207.0	1	2	1	0	1	2	8	6	1	3	0	0	25	
Noctuidae	<i>Acrionicta radcliffei</i>	9209.0	0	0	1	0	0	0	1	1	0	0	0	0	3	
Noctuidae	<i>Acrionicta grisea</i>	9212.0	8	7	46	9	37	11	24	24	6	43	6	4	225	
Noctuidae	<i>Acrionicta superans</i>	9226.0	0	1	0	0	0	1	1	4	0	0	0	0	7	
Noctuidae	<i>Acrionicta hasta</i>	9229.0	0	0	0	0	0	1	0	1	0	3	0	0	5	
Noctuidae	<i>Acrionicta fragilis</i>	9241.0	3	16	26	7	12	15	49	16	13	35	6	6	204	
Noctuidae	<i>Acrionicta impleta</i>	9257.0	1	7	9	3	4	7	10	5	8	10	1	4	69	
Noctuidae	<i>Acrionicta impressa</i>	9261.0	18	5	7	2	6	2	5	12	9	8	3	3	80	
Noctuidae	<i>Acrionicta obliquitata</i>	9272.0	7	0	10	2	3	0	1	3	2	6	1	1	36	
Noctuidae	<i>Sinyra henrici</i>	9280.0	0	0	0	0	0	0	0	1	0	0	0	0	1	
Noctuidae	<i>Harrissimenna trisignata</i>	9286.0	0	0	0	0	0	0	0	2	0	0	0	0	2	
Noctuidae	<i>Apamea amputatrix</i>	9348.0	1	2	0	1	0	1	0	0	0	0	0	1	6	
Noctuidae	<i>Apamea alia</i>	9351.0	1	0	0	0	2	0	1	0	0	0	2	0	6	
Noctuidae	<i>Apamea commoda</i>	9359.0	10	8	4	5	2	4	12	8	17	1	8	44	123	
Noctuidae	<i>Apamea sordens</i>	9364.0	0	3	2	0	1	0	0	0	2	1	2	3	14	

Family	Species	Checklist #	1999													TOTAL
			Site													
			27	43	44	60	61	73	82	83	86	98	126	127		
Noctuidae	<i>Apamea cogitata</i>	9367.1	88	63	15	22	26	12	20	13	35	7	79	127	507	
Noctuidae	<i>Apamea inficta</i>	9369.0	9	2	1	1	0	1	0	3	2	1	11	16	47	
Noctuidae	<i>Apamea niveivenosa</i>	9374.0	2	0	0	1	0	0	0	0	0	0	1	2	6	
Noctuidae	<i>Apamea devastator</i>	9382.0	5	1	0	0	1	2	2	0	5	1	3	15	35	
Noctuidae	<i>Luperina passer</i>	9391.0	2	1	1	0	0	2	6	0	3	0	3	4	22	
Noctuidae	<i>Eremobina claudens</i>	9396.0	5	0	4	0	1	1	1	0	1	0	1	3	17	
Noctuidae	<i>Oligia tonsa</i>	9413.0	15	2	0	2	2	2	16	5	9	0	6	13	72	
Noctuidae	<i>Oligia egens</i>	9417.0	2	0	0	0	0	0	0	0	0	0	0	0	2	
Noctuidae	<i>Oligia mactata</i>	9419.0	1	1	1	2	1	1	6	6	3	3	2	0	27	
Noctuidae	<i>Oligia illocata</i>	9420.0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Noctuidae	<i>Parastichtis suspecta</i>	9431.0	18	9	3	2	7	10	13	3	16	5	25	37	148	
Noctuidae	<i>Spartiniphaga includens</i>	9434.0	0	1	3	0	1	0	1	3	1	3	0	2	15	
Noctuidae	<i>Chortodes inquinata</i>	9437.0	25	4	6	3	3	3	2	10	8	4	2	5	75	
Noctuidae	<i>Chortodes rufostrigata</i>	9440.0	1	0	0	0	0	1	0	0	1	0	2	0	5	
Noctuidae	<i>Chortodes defecta</i>	9443.0	0	1	3	0	0	0	0	5	1	0	3	1	14	
Noctuidae	<i>Archanaara subflava</i>	9450.0	0	2	2	0	0	0	0	4	0	0	0	0	8	
Noctuidae	<i>Celaena reniformis</i>	9453.0	2	2	0	0	2	0	0	1	0	2	3	18	30	
Noctuidae	<i>Amphipoea interoceánica</i>	9456.0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Noctuidae	<i>Amphipoea americana</i>	9457.0	14	4	8	5	11	7	18	11	15	6	11	57	167	
Noctuidae	<i>Papaipema harrisi</i>	9472.0	5	45	12	1	30	17	10	12	14	20	10	18	194	
Noctuidae	<i>Hydraecia perobliqua</i>	9515.0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Noctuidae	<i>Bellura obliqua</i>	9525.0	1	1	2	1	3	0	1	1	0	0	0	0	10	
Noctuidae	<i>Euplexia benesimilis</i>	9545.0	9	7	3	1	8	4	14	7	4	9	4	27	97	
Noctuidae	<i>Phlogophora periculosa</i>	9547.0	2	2	8	3	3	4	6	2	4	3	7	6	50	
Noctuidae	<i>Enargia decolor</i>	9549.0	4	5	3	0	2	8	5	6	6	4	11	7	61	
Noctuidae	<i>Enargia infumata</i>	9550.0	2	5	0	1	1	1	4	2	0	1	0	2	19	
Noctuidae	<i>Ipimorpha pleonectusa</i>	9555.0	6	4	2	4	5	5	8	5	9	0	9	9	66	
Noctuidae	<i>Chytonix palliatricula</i>	9556.0	1	0	0	0	1	3	2	0	4	0	0	0	11	
Noctuidae	<i>Hyppa sp. nr. xylinoidea</i>	9578.1	0	0	0	0	1	0	3	0	0	3	0	1	8	
Noctuidae	<i>Aethes miranda</i>	9647.0	6	0	0	0	0	0	0	0	0	0	0	1	7	
Noctuidae	<i>Aethes mendosa</i>	9649.0	13	0	0	0	5	0	0	0	1	0	0	0	19	
Noctuidae	<i>Caradrina montana</i>	9656.0	6	4	0	0	0	0	0	4	0	0	2	7	23	

Family	Species	Checklist # ¹	1999													TOTAL
			Site													
			27	43	44	60	61	73	82	83	86	98	126	127		
Noctuidae	<i>Xylota curvicaula</i>	9874.0	0	1	0	0	0	0	0	0	1	0	1	0	3	
Noctuidae	<i>Lithomoia germana</i>	9878.0	0	0	0	0	0	0	1	0	0	0	0	0	4	
Noctuidae	<i>Homoglaea hircina</i>	9881.0	0	0	0	0	0	2	0	0	0	0	0	0	2	
Noctuidae	<i>Litholomia napaea</i>	9884.0	0	0	0	0	0	0	0	0	0	2	0	1	3	
Noctuidae	<i>Lithophane inominata</i>	9888.0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Noctuidae	<i>Euclitroedia pampina</i>	9952.0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Noctuidae	<i>Sunira bicolorago</i>	9957.0	0	0	0	0	0	0	1	0	0	0	0	0	1	
Noctuidae	<i>Sunira verberata</i>	9960.0	1	1	0	0	1	0	0	0	1	0	4	2	10	
Noctuidae	<i>Anathix puta</i>	9962.0	42	23	54	12	25	10	116	40	70	32	27	30	481	
Noctuidae	<i>Xanthia nr. togata</i>	9965.0	8	1	0	3	9	4	2	0	0	3	4	4	38	
Noctuidae	<i>Hillia iris</i>	9967.0	1	0	0	0	1	1	1	1	1	1	0	0	6	
Noctuidae	<i>Platypolia anceps</i>	9976.0	1	4	7	4	4	11	8	8	1	5	5	0	58	
Noctuidae	<i>Sutyna profunda</i>	9990.0	0	0	0	0	0	1	0	0	0	0	0	0	1	
Noctuidae	<i>Brachylomia populi</i>	9993.0	0	2	0	0	7	5	3	4	0	0	5	5	31	
Noctuidae	<i>Brachylomia algens</i>	9998.0	0	0	0	1	1	0	1	2	0	3	0	1	9	
Noctuidae	<i>Brachylomia discinigra</i>	9999.0	1	1	1	0	2	0	2	1	2	5	0	0	15	
Noctuidae	<i>Homohadena badistriga</i>	10059.0	0	0	1	0	0	1	2	2	0	1	0	0	7	
Noctuidae	<i>Homohadena infixa</i>	10065.0	0	0	0	0	0	0	4	1	0	1	3	1	10	
Noctuidae	<i>Cucullia intermedia</i>	10194.0	4	0	0	0	0	1	0	1	2	0	1	1	10	
Noctuidae	<i>Cucullia florea</i>	10197.0	0	0	0	0	0	0	0	1	0	0	0	1	2	
Noctuidae	<i>Discestra farnhami</i>	10232.0	2	0	0	0	0	0	0	1	0	0	0	1	4	
Noctuidae	<i>Mamestra configurata</i>	10271.0	0	0	0	0	2	0	1	0	2	0	0	1	6	
Noctuidae	<i>Mamestra curialis</i>	10272.0	0	0	0	0	0	1	1	0	0	0	0	1	3	
Noctuidae	<i>Polia nimbosa</i>	10275.0	2	6	5	1	10	5	6	5	5	7	5	8	65	
Noctuidae	<i>Polia imbrifera</i>	10276.0	27	28	30	22	46	20	24	25	39	35	29	45	370	
Noctuidae	<i>Polia purpurissata</i>	10280.0	3	0	0	0	1	1	0	0	2	1	2	3	13	
Noctuidae	<i>Orthodes goodelli</i>	10289.0	6	1	1	2	1	1	1	1	4	2	2	1	23	
Noctuidae	<i>Orthodes obscura</i>	10290.0	0	0	0	0	0	1	0	0	0	1	0	0	2	
Noctuidae	<i>Melanchra adjuncta</i>	10292.0	8	3	3	4	2	8	29	9	5	8	6	7	92	
Noctuidae	<i>Melanchra assimilis</i>	10295.0	2	0	0	0	0	2	0	0	1	1	0	0	6	
Noctuidae	<i>Lacanobia atlantica</i>	10297.0	15	19	1	1	3	3	4	2	19	4	10	13	94	
Noctuidae	<i>Lacanobia radix</i>	10298.0	27	11	18	8	33	9	39	11	21	19	38	66	300	

Family	Species	Checklist # ¹	1999													TOTAL
			Site													
			27	43	44	60	61	73	82	83	86	98	126	127		
Noctuidae	<i>Trichordestra lilacina</i>	10307.0	1	0	0	0	2	1	0	0	3	0	0	1	8	
Noctuidae	<i>Lacinipolia mediata</i>	10368.0	1	0	0	0	0	1	0	1	2	0	3	0	8	
Noctuidae	<i>Lacinipolia lustralis</i>	10370.0	0	0	1	0	1	0	1	1	2	0	0	1	7	
Noctuidae	<i>Lacinipolia anguina</i>	10372.0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Noctuidae	<i>Lacinipolia renigera</i>	10397.0	25	22	7	6	14	12	19	18	27	8	36	33	227	
Noctuidae	<i>Lacinipolia lorea</i>	10405.0	60	187	24	18	121	43	85	61	80	32	213	112	1036	
Noctuidae	<i>Lacinipolia olivacea</i>	10406.0	5	3	4	4	5	1	5	12	11	1	15	20	86	
Noctuidae	<i>Aletia oxygala</i>	10436.0	108	53	37	20	40	29	21	32	68	14	75	103	600	
Noctuidae	<i>Pseudaletia unipuncta</i>	10438.0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Noctuidae	<i>Leucania multilinea</i>	10446.0	25	5	1	1	5	9	4	13	11	2	6	17	99	
Noctuidae	<i>Leucania commoides</i>	10447.0	7	2	0	2	3	0	0	1	8	1	2	11	37	
Noctuidae	<i>Leucania insueta</i>	10449.0	6	2	0	0	2	0	0	2	17	0	2	14	45	
Noctuidae	<i>Orthostia revicta</i>	10490.0	3	1	8	1	8	11	1	0	2	13	0	0	48	
Noctuidae	<i>Orthostia hibisci</i>	10495.0	0	1	2	1	0	0	1	0	1	3	0	1	10	
Noctuidae	<i>Egira dolosa</i>	10513.0	0	0	0	2	2	0	0	0	0	0	0	0	4	
Noctuidae	<i>Nephelodes minians</i>	10524.0	13	2	3	5	3	4	1	7	13	4	23	7	85	
Noctuidae	<i>Protorthodes oviduca</i>	10563.0	9	5	3	0	2	5	5	2	5	5	6	11	58	
Noctuidae	<i>Agrotis venerabilis</i>	10651.0	1	0	0	1	1	1	2	0	0	1	1	0	8	
Noctuidae	<i>Agrotis volubilis</i>	10659.0	0	0	0	0	0	0	0	0	2	0	0	1	3	
Noctuidae	<i>Agrotis obliqua</i>	10660.0	0	2	0	1	0	0	0	1	0	0	1	2	7	
Noctuidae	<i>Feltia jaculifera</i>	10670.0	3	1	0	2	6	1	1	1	2	0	8	8	33	
Noctuidae	<i>Feltia herilis</i>	10676.0	73	4	10	2	40	15	16	27	81	4	45	60	377	
Noctuidae	<i>Euxoa divergens</i>	10702.0	3	0	1	2	2	0	1	3	1	0	6	1	20	
Noctuidae	<i>Euxoa auxiliaris</i>	10731.0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Noctuidae	<i>Euxoa intrita</i>	10749.0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Noctuidae	<i>Euxoa ochrogaster</i>	10801.0	0	5	0	0	1	0	1	0	3	0	2	14	26	
Noctuidae	<i>Euxoa castanea</i>	10826.1	2	0	0	0	0	0	0	0	2	0	1	1	6	
Noctuidae	<i>Euxoa servita</i>	10854.0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Noctuidae	<i>Euxoa ridingsiana</i>	10861.0	0	0	0	0	0	1	0	0	0	0	8	1	10	
Noctuidae	<i>Ochropleura implecta</i>	10891.0	23	9	5	10	4	1	0	9	17	10	16	12	116	
Noctuidae	<i>Diarsia rubifera</i>	10917.0	12	7	9	7	3	14	112	41	28	9	34	35	311	
Noctuidae	<i>Diarsia rosaria</i>	10921.0	4	1	2	0	3	1	2	0	0	0	0	0	13	

Family	Species	Checklist # ¹	1999												TOTAL
			Site												
			27	43	44	60	61	73	82	83	86	98	126	127	
Noctuidae	<i>Spaelotis clandesitina</i>	10926.0	0	1	0	0	2	1	0	3	2	1	0	2	12
Noctuidae	<i>Graphiphora augur</i>	10928.0	22	17	2	6	7	7	11	8	6	6	52	35	179
Noctuidae	<i>Eurois occulta</i>	10929.0	7	55	10	12	13	6	4	20	6	11	24	52	220
Noctuidae	<i>Eurois astricta</i>	10930.0	5	6	7	4	8	3	8	13	4	22	8	8	96
Noctuidae	<i>Xestia c-nigrum</i>	10942.0	76	24	6	8	25	14	24	28	51	14	101	134	505
Noctuidae	<i>Xestia normaniana</i>	10943.0	9	4	0	0	5	3	19	0	11	2	9	7	69
Noctuidae	<i>Xestia smithii</i>	10944.0	19	18	5	4	11	13	8	14	22	4	27	44	189
Noctuidae	<i>Pseudohemermonassa tenuicula</i>	10951.0	22	24	6	7	15	2	3	1	37	3	27	43	190
Noctuidae	<i>Agnorisma bugrai</i>	10954.0	0	0	0	0	1	1	0	0	0	0	0	1	3
Noctuidae	<i>Coenophila opacifrons</i>	10988.0	1	0	0	0	0	0	1	0	0	0	0	0	2
Noctuidae	<i>Paradiarsia littoralis</i>	10992.0	6	1	0	2	2	3	1	6	5	1	6	2	35
Noctuidae	<i>Cerastis salicarium</i>	10996.0	0	0	2	0	0	0	0	0	0	0	0	0	2
Noctuidae	<i>Anaplectoides prasina</i>	11000.0	0	10	3	0	3	0	5	2	3	4	6	0	36
Noctuidae	<i>Anaplectoides pressus</i>	11001.0	3	3	6	1	8	6	35	13	8	11	7	11	112
Noctuidae	<i>Chersotis juncta</i>	11003.0	0	0	0	0	0	0	0	0	1	0	0	0	1
Noctuidae	<i>Protalampra rufipectus</i>	11004.0	9	1	2	1	3	1	5	0	3	0	1	2	28
Noctuidae	<i>Euretiagrotis perattenta</i>	11008.0	18	21	14	6	47	13	47	36	22	19	24	11	278
Noctuidae	<i>Cryptocala acadensis</i>	11012.0	11	1	1	1	6	12	3	2	2	2	1	11	53
Noctuidae	<i>Abagrotis placida</i>	11041.0	3	1	0	0	2	0	0	0	0	0	0	0	6
Noctuidae	<i>Pyrrhia exprimens</i>	11064.0	0	1	0	0	0	0	0	0	1	0	0	0	2

1 - Check list numbers follow those of Hodges *et al.* (1983).

APPENDIX B.
Summary of 2000 trap catch by site.

Family	Species	Checklist #	2000																	TOTAL							
			21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5		86.0	87.0	98.0	100.5	126.0	127.0	139.0
He	<i>Sthenopis purpurascens</i>	19.0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	5
He	<i>Korscheltellus gracilis</i>	31.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3	5
Dr	<i>Habrosyne scripta</i>	6235.0	0	0	1	4	0	1	0	0	3	2	1	3	0	1	0	1	0	2	0	2	0	4	0	2	27
Dr	<i>Pseudothyatira cymatophoroides</i>	6237.0	2	1	0	2	0	0	0	1	0	0	0	3	2	0	3	5	0	2	0	5	1	0	1	2	30
Dr	<i>Euthyatira pudens</i>	6240.0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Dr	<i>Drepana arcuata</i>	6251.0	1	0	0	2	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	9
Dr	<i>Drepana bilineata</i>	6252.0	1	0	0	3	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	6
Dr	<i>Eudeilinea herminia</i>	6253.0	2	1	0	1	3	0	0	0	0	4	1	2	5	2	0	0	1	0	1	0	3	2	1	0	29
Dr	<i>Oreta rosea</i>	6255.0	0	0	0	3	1	1	0	0	2	1	1	0	3	0	3	1	0	0	0	1	1	2	0	6	26
Ge	<i>Protitame virginalis</i>	6270.0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	1	0	1	0	3	1	0	2	11
Ge	<i>Itame sulphurea</i>	6283.0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ge	<i>Itame loricaria</i>	6290.0	2	3	0	2	0	0	2	1	0	0	3	0	1	0	0	0	0	0	4	1	2	6	1	3	35
Ge	<i>Semiothisa aemulataria</i>	6326.0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ge	<i>Iridopsis larvata</i>	6588.0	0	1	0	8	4	3	0	0	2	0	1	0	2	0	1	0	0	2	0	3	0	4	0	5	36
Ge	<i>Ectropis crepuscularia</i>	6597.0	0	0	0	4	0	2	0	1	1	0	0	7	0	0	0	0	1	0	2	0	2	0	1	0	19
Ge	<i>Protoboarmia porcelaria</i>	6598.0	0	0	0	0	1	2	1	0	0	2	2	1	2	2	1	1	1	1	3	1	9	3	0	0	34
Ge	<i>Biston betularia</i>	6640.0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	0	6	2	15
Ge	<i>Cabera erythemaria</i>	6677.0	96	115	14	33	45	27	13	43	18	120	102	45	24	30	16	35	30	36	99	205	91	123	41	76	1477
Ge	<i>Cabera variolaria</i>	6678.0	31	24	2	8	8	9	6	10	6	27	25	14	11	44	5	15	2	21	55	68	18	66	19	46	540
Ge	<i>Euchlaena obtusaria</i>	6726.0	6	8	0	2	9	4	6	2	5	7	3	10	7	9	7	7	0	3	3	17	2	5	3	6	131
Ge	<i>Euchlaena johnsonaria</i>	6729.0	1	1	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	0	0	1	0	0	8
Ge	<i>Euchlaena marginaria</i>	6734.0	2	0	0	7	1	1	0	0	1	1	0	5	0	0	2	0	0	0	0	2	0	1	1	0	24
Ge	<i>Euchlaena tigrinaria</i>	6737.0	5	6	1	4	7	2	2	7	2	10	2	2	5	3	5	5	1	5	6	10	11	6	9	13	129

Checklist # 2

2000

1

Family	Species	Checklist	Site																									
			21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0	TOTA	
Ge	<i>Xanthotype urticaria</i>	6740.0	1	3	0	0	1	0	1	0	0	4	1	2	1	2	0	3	0	0	3	3	4	0	4	4	37	
Ge	<i>Xanthotype sospeta</i>	6743.0	1	3	0	1	10	4	4	1	3	3	1	13	2	6	2	6	1	6	8	12	1	9	1	3	101	
Ge	<i>Pero morrisonaria</i>	6755.0	14	4	1	32	6	12	7	7	15	17	7	38	9	5	43	16	7	19	16	28	17	7	24	26	377	
Ge	<i>Campaea perlata</i>	6796.0	8	18	1	4	1	1	3	4	3	1	6	4	22	5	4	6	4	1	6	11	10	9	8	17	157	
Ge	<i>Metanema inatomaria</i>	6819.0	1	1	0	4	1	1	3	1	0	6	1	1	3	9	3	1	1	3	3	6	9	5	2	4	69	
Ge	<i>Metanema determinata</i>	6820.0	11	4	1	4	4	3	2	5	5	6	1	3	4	7	5	3	2	4	5	9	8	3	4	111		
Ge	<i>Metarranthis diuaria</i>	6822.0	17	5	0	12	3	12	2	6	13	17	2	21	6	8	4	0	4	9	1	15	9	14	4	9	193	
Ge	<i>Anogoga occidentaria</i>	6836.0	2	1	0	7	0	5	0	6	2	5	0	4	0	0	1	0	1	4	2	10	4	4	2	3	63	
Ge	<i>Probole amitaria</i>	6838.0	13	4	2	25	12	9	4	8	7	26	5	30	20	11	11	4	7	19	11	35	18	17	11	14	323	
Ge	<i>Plagodis phlogosaria</i>	6842.0	2	1	0	9	1	3	0	0	4	2	1	3	3	0	4	0	1	0	3	0	2	2	0	0	41	
Ge	<i>Plagodis alchoolaria</i>	6844.0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
Ge	<i>Besma quercivoraria</i>	6885.0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	
Ge	<i>Sycia macularia</i>	6912.0	4	0	0	4	1	3	0	2	3	0	2	3	0	0	4	2	0	1	2	8	1	6	4	5	55	
Ge	<i>Tetracis crocallata</i>	6963.0	5	0	3	4	6	3	0	1	6	5	0	15	5	3	4	2	4	4	2	11	10	2	2	4	101	
Ge	<i>Prochoerodes transversata</i>	6982.0	23	13	2	40	4	17	4	9	22	15	0	46	1	2	25	13	11	8	3	41	3	8	14	22	346	
Ge	<i>Nematocampa resistaria</i>	7009.0	5	0	0	8	4	1	2	0	3	1	10	0	3	0	3	0	1	4	0	9	2	2	0	8	64	
Ge	<i>Nemoria unitaria</i>	7018.0	0	0	0	1	1	1	0	0	0	0	0	0	8	4	1	4	1	1	10	5	4	9	1	4	55	
Ge	<i>Nemoria mimosaria</i>	7048.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	4	
Ge	<i>Synchlora aerata</i>	7058.0	4	2	0	2	0	0	0	1	0	0	0	0	3	1	1	1	0	0	2	0	0	1	0	1	19	
Ge	<i>Idaea rotundopennata</i>	7125.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Ge	<i>Cyclophora pendulinaria</i>	7139.0	4	0	0	5	1	1	1	0	0	3	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Ge	<i>Scopula limboundata</i>	7159.0	5	0	0	10	0	1	0	0	1	0	0	2	2	1	4	7	1	1	4	2	5	6	2	19	2	19
Ge	<i>Scopula junctaria</i>	7164.0	17	4	2	6	15	2	6	1	5	36	14	12	21	30	9	8	1	26	20	15	18	27	14	27	336	
Ge	<i>Scopula frigidaria</i>	7166.0	14	0	2	2	14	4	3	11	2	3	1	3	1	3	2	2	1	1	1	1	0	0	2	2	75	
Ge	<i>Scopula inductata</i>	7169.0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	3	
Ge	<i>Dysstroma citrata</i>	7182.0	12	21	5	41	16	11	2	4	6	8	7	18	13	4	11	10	6	6	4	24	2	15	29	28	303	

Family	Species	Checklist # ²	2000																				TOTAL				
			21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0		100.5	126.0	127.0	139.0
Nc	<i>Phalaenophana pyramusalis</i>	8338.0	0	0	0	2	1	1	1	2	2	3	0	2	2	0	2	0	4	2	2	2	2	3	1	1	35
Nc	<i>Zanclognatha lutealba</i>	8354.0	10	15	2	21	6	5	9	3	13	12	24	8	49	25	32	31	17	47	35	35	49	45	24	80	597
Nc	<i>Chytolita petrealis</i>	8356.0	44	13	16	32	17	13	26	26	9	31	13	36	27	10	6	5	15	24	18	18	18	35	13	24	489
Nc	<i>Macrochilo bivittata</i>	8359.0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	4	
Nc	<i>Macrochilo louisiana</i>	8361.0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Nc	<i>Phalaenostola metonalis</i>	8362.0	6	1	0	12	3	0	1	2	1	7	14	2	10	13	11	18	5	14	16	14	14	18	12	17	211
Nc	<i>Phalaenostola hanhami</i>	8365.0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	1	0	8	
Nc	<i>Palthis angulalis</i>	8397.0	4	7	3	9	10	6	2	6	7	5	2	2	10	5	3	4	3	4	2	8	8	3	6	2	121
Nc	<i>Rivula propinqualis</i>	8404.0	7	3	0	9	12	9	1	6	1	2	17	4	35	14	10	18	2	14	7	19	8	21	10	33	262
Nc	<i>Mycterophora inexplicata</i>	8413.0	0	0	0	1	0	0	0	1	0	0	0	3	0	2	3	1	0	2	3	0	3	2	1	22	
Nc	<i>Hypena palparia</i>	8444.0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	3
Nc	<i>Hypena atomaria</i>	8450.0	0	0	0	1	2	3	0	0	0	6	1	3	0	2	0	1	0	4	3	3	4	1	3	2	39
Nc	<i>Hypena edictalis</i>	8452.0	0	2	1	4	21	4	1	0	1	4	1	3	3	2	10	0	6	9	7	21	6	30	6	28	170
Nc	<i>Lomanthes eductalis</i>	8455.0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
Nc	<i>Scoliopteryx libatrix</i>	8555.0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	5
Nc	<i>Zale minerea</i>	8697.0	7	3	0	15	0	1	1	1	4	7	0	8	0	0	2	1	0	5	0	3	0	0	0	4	62
Nc	<i>Euclidia cuspidata</i>	8731.0	2	0	0	1	0	2	0	1	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	13
Nc	<i>Caenurgina crassiuscula</i>	8738.0	3	1	0	5	0	0	1	2	0	0	0	0	0	6	0	0	1	0	3	0	0	1	1	1	25
Nc	<i>Caenurgina erechthea</i>	8739.0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Nc	<i>Catocala relicta</i>	8803.0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	
Nc	<i>Catocala unijuga</i>	8805.0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	1	2	0	0	0	1	0	0	1	0	10
Nc	<i>Catocala briseis</i>	8817.0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	4
Nc	<i>Catocala semirelicta</i>	8821.0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	6
Nc	<i>Catocala blandula</i>	8867.0	0	0	0	3	0	0	0	2	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	8
Nc	<i>Abrostola urentis</i>	8881.0	2	2	0	4	4	2	2	2	1	7	1	5	3	3	5	2	0	6	3	6	0	2	2	6	70
Nc	<i>Diachrysia aereoides</i>	8896.0	11	2	1	26	12	9	3	8	3	0	2	21	11	1	15	12	3	7	4	11	7	4	12	11	196

Family	Species	Checklist #	2000																		
			Site																		

	21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0	TOTAL	
Nc <i>Diachrysia balluca</i>	8897.0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Nc <i>Eosphoropteryx thuytoides</i>	8905.0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Nc <i>Autographa rubida</i>	8909.0	1	1	0	3	1	1	0	1	2	1	0	1	2	5	2	0	2	0	0	0	1	3	1	29	
Nc <i>Autographa bimaculata</i>	8911.0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	7	
Nc <i>Autographa mappa</i>	8912.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	
Nc <i>Autographa pseudogamma</i>	8913.0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	4	
Nc <i>Autographa californica</i>	8914.0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Nc <i>Autographa flagellum</i>	8916.0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Nc <i>Autographa ampla</i>	8923.0	1	1	0	1	0	2	0	0	0	0	3	0	0	2	1	0	0	0	0	0	0	0	1	3	
Nc <i>Anagrapha falcifera</i>	8924.0	1	1	0	3	2	0	2	4	0	3	1	2	1	1	0	0	1	1	1	1	2	4	0	31	
Nc <i>Syngrapha octoscripta</i>	8926.0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	3	
Nc <i>Syngrapha viridisigma</i>	8929.0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Nc <i>Plusia putnami</i>	8950.0	9	0	5	2	5	1	1	5	4	0	0	8	2	2	1	0	5	0	0	0	0	0	0	53	
Nc <i>Plusia venusta</i>	8953.0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	4	0	1	0	1	3	0	0	14	
Nc <i>Baileya ophthalmica</i>	8970.0	0	0	0	4	0	2	0	6	3	0	2	3	0	0	0	0	1	0	5	0	0	0	0	26	
Nc <i>Nola cilioides</i>	8990.0	1	0	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	3	1	0	0	0	9	
Nc <i>Pseudeva purpurigera</i>	8999.0	0	1	0	2	0	0	0	0	0	0	1	0	0	0	0	3	0	0	5	1	2	2	2	19	
Nc <i>Lithacodia albidula</i>	9048.0	41	19	9	30	13	15	1	12	7	29	15	47	21	16	11	16	56	13	28	18	39	20	34	520	
Nc <i>Lithacodia carneola</i>	9053.0	1	4	0	2	4	0	0	1	0	2	2	1	8	5	11	0	0	1	0	17	1	1	1	62	
Nc <i>Raphia frater</i>	9193.0	86	120	34	184	12	82	50	86	53	58	37	58	39	57	62	28	24	117	15	43	64	40	79	105	1533
Nc <i>Acrionicta dactylina</i>	9203.0	2	2	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	10	
Nc <i>Acrionicta vulpina</i>	9206.0	0	0	0	0	1	1	2	2	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	10	
Nc <i>Acrionicta innotata</i>	9207.0	12	0	0	15	4	1	0	2	3	1	6	2	1	16	7	0	2	0	4	0	0	0	0	76	
Nc <i>Acrionicta grisea</i>	9212.0	32	8	6	53	6	40	11	4	19	39	2	27	9	4	12	7	2	20	2	31	9	7	11	362	
Nc <i>Acrionicta superans</i>	9226.0	2	0	0	3	0	1	0	1	1	0	2	0	1	1	1	0	1	1	0	0	2	0	1	18	
Nc <i>Acrionicta hasta</i>	9229.0	1	0	0	1	0	0	1	0	2	0	1	0	0	0	0	0	0	1	2	1	0	0	0	10	

2000

Family Species

Site

	21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0	TOTAL	
Nc <i>Acronicta fragilis</i>	9241.0	22	4	1	72	3	20	20	7	10	24	2	18	12	4	25	10	7	14	5	20	8	14	8	9	339
Nc <i>Acronicta impleta</i>	9257.0	14	5	3	20	3	5	0	0	9	5	1	7	1	1	6	4	1	6	0	4	1	3	3	1	103
Nc <i>Acronicta impressa</i>	9261.0	6	11	5	11	0	4	3	3	5	9	5	8	6	2	2	2	2	13	0	7	5	5	2	4	120
Nc <i>Acronicta obliuina</i>	9272.0	6	10	2	12	0	9	0	5	2	8	1	2	1	13	2	14	3	2	1	17	3	3	1	1	118
Nc <i>Simyra henrici</i>	9280.0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3
Nc <i>Harrissimenna trisignata</i>	9286.0	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	2	0	1	0	2	0	0	0	0	9
Nc <i>Apamea lignicolora</i>	9333.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	6
Nc <i>Apamea amputatrix</i>	9348.0	0	1	0	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	6
Nc <i>Apamea alia</i>	9351.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	
Nc <i>Apamea commoda</i>	9359.0	20	6	6	28	2	0	9	9	3	1	24	3	26	28	2	2	0	23	13	5	26	7	29	36	308
Nc <i>Apamea sordens</i>	9364.0	0	1	0	0	1	0	0	2	0	1	0	0	0	0	1	0	1	0	0	1	13	0	2	0	23
Nc <i>Apamea nr. lateritia</i>	9365.0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	4	
Nc <i>Apamea cogitata</i>	9367.1	87	61	163	58	64	11	40	110	60	9	58	25	107	183	5	25	15	19	95	15	90	121	105	80	1606
Nc <i>Apamea inficita</i>	9369.0	8	4	15	6	1	2	1	4	2	2	3	0	17	11	3	4	1	6	7	2	11	8	8	10	136
Nc <i>Apamea niveivenosa</i>	9374.0	0	3	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	4	0	0	0	2	0	14	
Nc <i>Apamea devastator</i>	9382.0	8	12	49	9	6	1	7	8	1	2	1	1	9	5	1	0	5	5	24	0	19	6	14	5	198
Nc <i>Luperina passer</i>	9391.0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	
Nc <i>Eremobina claudens</i>	9396.0	0	17	4	13	2	0	0	26	2	1	0	1	0	0	1	1	14	0	0	0	3	0	3	2	90
Nc <i>Oligia tonsa</i>	9413.0	1	10	1	2	0	0	0	3	0	0	3	0	3	1	1	2	0	0	1	0	2	2	5	4	41
Nc <i>Oligia egens</i>	9417.0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Nc <i>Oligia mactata</i>	9419.0	8	2	1	12	2	0	0	3	1	0	1	3	1	0	1	0	2	1	0	0	1	0	7	3	49
Nc <i>Oligia illocata</i>	9420.0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	
Nc <i>Parasichtis suspecta</i>	9431.0	7	4	2	13	11	4	4	4	0	1	4	0	4	2	8	2	2	1	1	0	2	1	17	2	96
Nc <i>Spartimiphaga includens</i>	9434.0	0	6	0	0	3	1	0	2	2	0	0	0	0	0	0	1	0	2	1	0	0	1	1	2	22
Nc <i>Chortodes inquinata</i>	9437.0	3	9	2	3	0	1	0	1	1	1	3	4	5	10	2	6	2	6	9	6	2	4	1	3	84
Nc <i>Chortodes rufostriata</i>	9440.0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	3	5	15

Family	Species	Checklist #	2000																										TOTAL
			21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0			
Nc	<i>Chortodes basistriga</i>	9440.0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	
Nc	<i>Chortodes defecta</i>	9443.0	0	1	0	1	0	0	0	1	0	0	0	1	2	2	0	2	0	2	0	2	0	1	0	0	0	13	
Nc	<i>Archanaara subflava</i>	9450.0	1	7	2	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	0	2	0	0	18	
Nc	<i>Celaena reniformis</i>	9453.0	1	2	0	4	1	0	0	1	1	0	0	1	0	0	0	1	0	1	1	1	0	1	0	6	1	22	
Nc	<i>Amphipoea interoceana</i>	9456.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2		
Nc	<i>Amphipoea americana</i>	9457.0	3	63	57	19	6	3	3	5	6	24	16	6	17	6	8	9	4	4	10	11	4	7	8	61	17	373	
Nc	<i>Papaipema hartisii</i>	9472.0	1	4	4	0	17	2	3	5	2	15	2	7	0	5	0	0	5	3	1	7	3	6	9	12	113		
Nc	<i>Hydraecia perobliqua</i>	9515.0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
Nc	<i>Bellura obliqua</i>	9525.0	2	4	4	3	1	6	0	31	4	1	0	8	2	5	0	4	2	0	3	2	6	2	0	4	94		
Nc	<i>Euplexia benesimilis</i>	9545.0	2	3	1	4	3	0	1	3	1	5	0	0	1	1	4	3	0	3	3	2	8	5	8	0	61		
Nc	<i>Phlogophora periculosa</i>	9547.0	16	3	0	27	4	6	4	2	6	1	2	5	10	1	7	6	1	1	1	3	7	10	9	8	10	149	
Nc	<i>Enargia decolor</i>	9549.0	7	9	6	18	6	2	5	5	2	2	4	11	4	1	8	0	12	3	2	7	5	10	9	6	144		
Nc	<i>Enargia infumata</i>	9550.0	2	0	0	3	0	0	0	0	4	0	0	0	1	0	1	0	0	0	0	1	0	0	0	3	15		
Nc	<i>Ipimorpha pleonectusa</i>	9555.0	0	0	0	4	1	0	2	2	4	1	4	5	2	0	1	4	6	1	1	7	4	3	5	3	60		
Nc	<i>Chytonix palliatricula</i>	9556.0	1	0	0	6	0	2	2	0	4	0	0	0	0	0	2	0	0	1	0	0	1	1	0	0	20		
Nc	<i>Andropolis contacta</i>	9564.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		
Nc	<i>Hyppa nr. xylinoidea</i>	9578.0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	8		
Nc	<i>Amphipyra tragopoginis</i>	9639.0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2		
Nc	<i>Athetis miranda</i>	9647.0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	5		
Nc	<i>Athetis mendosa</i>	9649.0	0	11	0	0	1	0	0	0	0	5	0	0	0	0	0	0	0	0	1	2	0	1	0	0	21		
Nc	<i>Caradrina montana</i>	9656.0	1	13	3	5	2	0	2	1	2	1	0	1	6	0	2	0	2	0	16	0	3	1	11	3	75		
Nc	<i>Xylena cineritii</i>	9876.0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
Nc	<i>Lithomoia germana</i>	9878.0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4		
Nc	<i>Litholomia napaea</i>	9884.0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3		
Nc	<i>Lithophane inominata</i>	9888.0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
Nc	<i>Eucitroedia pampina</i>	9952.0	0	0	0	8	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	13		

Family

Species

Site

	21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0	TOTAL
Nc <i>Sunira verberata</i>	9960.0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	0	0	1	0	0	0	1	11	2	22
Nc <i>Anathix puta</i>	9962.0	12	133	28	45	9	3	11	7	18	16	38	12	3	25	17	15	39	8	21	15	29	65	87	683
Nc <i>Xanthia nr. togata</i>	9965.0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	5	0	11
Nc <i>Hillia iris</i>	9967.0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4
Nc <i>Sutyna profunda</i>	9990.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Nc <i>Brachylomia populi</i>	9993.0	7	6	0	1	0	1	1	1	0	3	0	1	3	0	2	0	2	0	1	1	3	5	4	45
Nc <i>Brachylomia algens</i>	9998.0	3	7	0	4	0	2	2	1	1	1	4	0	0	0	1	1	1	1	1	7	1	0	2	41
Nc <i>Brachylomia discinigra</i>	9999.0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	5
Nc <i>Homohadena badistriga</i>	10059.0	1	1	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6
Nc <i>Homohadena stabilis</i>	10062.0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Nc <i>Homohadena infixa</i>	10065.0	4	0	0	11	0	1	1	0	1	0	3	0	0	1	1	0	0	0	2	2	0	1	1	29
Nc <i>Cucullia intermedia</i>	10194.0	1	0	2	0	0	0	1	0	0	1	0	1	0	0	0	0	2	0	0	0	0	0	0	8
Nc <i>Diseastra farnhami</i>	10232.0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Nc <i>Polia nimbo</i>	10275.0	2	0	0	3	2	0	0	0	4	2	1	1	3	3	3	1	2	0	3	9	1	3	7	50
Nc <i>Polia imbrifera</i>	10276.0	17	10	0	18	1	6	4	8	2	4	16	8	19	18	7	12	12	11	10	32	33	20	35	352
Nc <i>Polia purpurissata</i>	10280.0	0	2	0	1	0	2	0	0	0	0	1	0	0	0	0	0	1	2	1	1	1	1	1	14
Nc <i>Orthodes goodelli</i>	10289.0	0	0	0	0	0	0	0	0	0	3	0	0	2	0	1	1	1	1	0	3	5	0	2	18
Nc <i>Orthodes obscura</i>	10290.0	0	1	0	2	1	0	0	2	2	2	0	0	1	0	0	1	1	0	0	0	1	0	2	20
Nc <i>Melanchra adjuncta</i>	10292.0	5	1	1	11	0	4	3	1	1	1	3	3	5	3	3	0	1	1	3	1	2	1	6	61
Nc <i>Melanchra assimilis</i>	10295.0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5
Nc <i>Lacanobia atlantica</i>	10297.0	1	4	19	1	2	3	3	2	0	3	2	8	8	0	0	3	7	1	1	37	12	19	13	151
Nc <i>Lacanobia radix</i>	10298.0	8	5	2	16	1	1	1	3	4	4	6	5	1	14	4	4	5	5	9	24	6	32	16	179
Nc <i>Trichordestra lilacina</i>	10307.0	0	1	4	1	0	1	0	1	0	1	1	0	1	0	0	1	2	4	0	1	2	1	0	23
Nc <i>Lacinipolia meditata</i>	10368.0	3	2	3	5	1	0	2	0	2	2	0	14	3	0	1	4	1	2	0	5	4	4	1	59
Nc <i>Lacinipolia lustralis</i>	10370.0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	6
Nc <i>Lacinipolia renigera</i>	10397.0	24	31	26	16	16	13	23	46	10	7	61	16	93	157	2	15	8	30	148	8	77	98	37	1028

2000

Checklist # 2

1

Family Species

Site

	21.0	27.0	35.5	39.0	43.0	44.0	54.5	59.5	60.0	61.0	63.5	73.0	78.0	79.0	82.0	83.0	85.5	86.0	87.0	98.0	100.5	126.0	127.0	139.0	TOTA	
Nc <i>Laciniipolia lorea</i>	10405.0	22	63	30	23	123	8	32	28	6	24	41	32	112	52	46	35	31	40	60	33	159	121	75	69	1265
Nc <i>Laciniipolia olivacea</i>	10406.0	3	13	15	16	1	3	12	6	3	9	7	9	15	17	1	10	5	7	23	2	16	8	22	54	277
Nc <i>Faronta diffusa</i>	10431.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Nc <i>Aletia oxygala</i>	10436.0	35	98	178	26	60	23	38	88	24	17	38	25	129	117	8	45	33	43	129	14	52	72	50	44	1386
Nc <i>Pseudaletia unipuncta</i>	10438.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Nc <i>Leucania multilinea</i>	10446.0	0	10	4	1	3	3	3	0	3	0	5	1	5	5	0	1	0	10	4	0	3	2	5	6	74
Nc <i>Leucania commoides</i>	10447.0	3	4	4	4	1	0	0	1	0	1	1	0	3	9	0	4	2	7	1	2	8	8	4	2	69
Nc <i>Leucania insueta</i>	10449.0	2	0	6	2	0	0	1	0	0	1	2	0	3	0	0	0	1	16	0	0	4	5	2	4	49
Nc <i>Orthosia revicta</i>	10490.0	0	1	0	4	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	9
Nc <i>Nephelodes minians</i>	10524.0	1	12	8	8	0	0	2	9	2	2	0	0	5	6	0	0	3	9	2	0	2	7	12	0	90
Nc <i>Protorthodes oviduca</i>	10563.0	9	5	14	20	19	1	17	4	0	1	2	5	27	1	3	1	5	6	2	2	9	10	3	5	171
Nc <i>Agrotis venerabilis</i>	10651.0	8	26	12	24	12	1	1	2	2	5	1	6	3	2	0	0	6	3	7	0	0	3	6	2	132
Nc <i>Agrotis stigmosa</i>	10658.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Nc <i>Agrotis volubilis</i>	10659.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	3
Nc <i>Agrotis obliqua</i>	10660.0	0	3	2	1	0	1	0	1	0	1	0	1	1	0	1	0	1	0	2	0	1	0	1	1	18
Nc <i>Feltia jaculifera</i>	10670.0	1	2	7	6	1	0	4	1	1	7	0	1	3	9	0	0	8	1	13	0	1	1	2	3	72
Nc <i>Feltia herilis</i>	10676.0	23	45	25	32	7	3	31	53	6	19	13	29	34	39	8	13	26	23	29	4	15	30	16	43	566
Nc <i>Euxoa divergens</i>	10702.0	0	0	2	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1	2	0	2	1	0	2	14
Nc <i>Euxoa tristicta</i>	10723.0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3
Nc <i>Euxoa auxiliaris</i>	10731.0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	6	
Nc <i>Euxoa intrita</i>	10749.0	0	4	2	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	11
Nc <i>Euxoa campestris</i>	10756.0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	3
Nc <i>Euxoa basalis</i>	10798.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	5	
Nc <i>Euxoa ochrogaster</i>	10801.0	1	7	2	19	0	0	4	8	0	2	8	2	3	0	3	0	63	4	27	1	8	1	35	18	216
Nc <i>Euxoa tessellata</i>	10805.0	3	15	38	11	0	1	5	18	1	7	1	2	6	0	0	0	15	3	31	0	14	4	22	22	219
Nc <i>Euxoa castanea</i>	10826.1	5	11	14	3	0	0	2	2	2	1	4	1	8	7	0	1	6	3	16	0	3	6	6	13	114

Family	Species	Checklist #	2000																				TOTAL				
			Site																								
Nc	<i>Cryptocala acadiensis</i>	11012.0	39	27	9	0	3	23	4	16	7	1	6	10	2	4	4	1	2	6	1	11	8	2	10	14	139.0
Nc	<i>Abagrotis placida</i>	11041.0	1	6	1	3	0	0	1	1	1	1	2	2	0	1	2	0	11	6	8	2	2	1	2	4	58
Nc	<i>Pyrrhia exprimens</i>	11064.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
																							210				
																							58				
																							1				

1 He = Hepialidae, Dr = Drepanidae, Ge = Geometridae, Ur = Uranidae, La = Lasiocampidae, Sa = Saturniidae, Sp = Sphingidae, Nt = Notodontidae, Ar = Arctidae, Ly = Lymantriidae, Nc = Noctuidae.

2 Numbers correspond to Hodges (1981).

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